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A TAXONOMIC STUDY OF WESTERN CANADIAN SPECIES IN THE GENUS *BETULA*

by

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The undersigned certify that they have read and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "A TAXONOMIC STUDY OF WESTERN CANADIAN SPECIES IN THE GENUS BETULA", submitted by Janet Rogge Dugle in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

Five western North American birches, *Betula fontinalis*, *B. glandulosa*, *B. pumila* var. *glandulifera*, *B. resinifera* and *B. papyrifera* are studied taxonomically. Synonymy, descriptions, distribution and representative specimens examined are included. Four hybrid taxa, *B.* x *winteri*, *B.* x *sargentii*, *B.* x *arbuscula*, and *B.* x *uliginosa*, are described for the first time and three additional hybrids, *B.* x *utahensis*, *B.* x *eastwoodae* and *B.* x *sandbergii* are also included.

When birch species are in contact, they often hybridize. The populations so formed have been analyzed and the nature of several hybrid entities determined. The methods of analysis applied are as follows: chromatography of leaves and bark; hybrid index; polygonal graphs; chromosome numbers; pollen size, morphology and stainability; stomatal size; germination data; and pictorialized scatter diagrams. *Betula* x *uliginosa* (2n = 28-56) is the result of hybridization between *B. resinifera* and *B. pumila* var. *glandulifera*. In the population analyzed, introgression was in the direction of *B. pumila* var. *glandulifera*, the birch with the higher chromosome number. When *B. pumila* var. *glandulifera* is in contact with *B. glandulosa*, *B.* x *sargentii* (2n = 28-56) is produced. Introgression seems to be in both directions, although most of the gene flow

is in the direction of the taxon with the higher chromosome number, B. pumila var. glandulifera. B. x eastwoodae (2n = 28) is the result of hybridization between B. glandulosa and B. fontinalis. Introgression was influenced very little by environmental selection, and B. x eastwoodae seemed to be as common as either of the parental species; and any gene flow was in either direction. B. x utahensis (2n = 28-84 with a concentration at 2n = 56) is the result of hybridization between B. papyrifera and B. fontinalis. In populations of these birches, introgression is mainly from B. fontinalis into B. papyrifera. Hybridization of B. x sargentii and B. papyrifera results in B. x arbuscula (2n = 28-84), a rare hybrid. Tentative conclusions are that introgression is in the direction of B. papyrifera, the taxon with the higher chromosome number. Hybridization of B. resinifera and B. papyrifera produces B. x winteri (2n = 28-84 with a concentration of individuals at 2n = 56). In the populations of these birches which were analyzed, introgression was in both directions. B. x sandbergii (2n = 56-84) results from hybridization of B. papyrifera and B. pumila var. glandulifera. As contrasted with the above, and probably as a result of strong environmental influence in the area in which this cross was analyzed, introgression was in the direction of B. pumila var. glandulifera, the parental taxon with the lower chromosome number.

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INTRODUCTION

A NOTE OF EXPLANATION ON THE FORMAT OF THE THESIS

Taxonomy may be defined as the study of the principles and practice of classification, and it has come to be applied primarily to the methods, principles and results of biological classification (Heslop-Harrison, 1953). Davis and Heywood (1963) present a similar but more limited definition: "Taxonomy is the study of classification including its bases, principles, procedures, and rules." Taxonomy, classification, identification, and nomenclature are all included by these authors in "Systematics". In contrast to this view, Mason (1950) has defined taxonomy as a synthesis of interrelationships. Four major phases are distinguished: documentation, nomenclature, taxonomic system, and the systematic or fact-finding phase.

The methods applied in the systematic or fact-finding phase are constantly changing (Valentine and Löve, 1958) and the results are often incorporated in the formal taxonomic system. Valentine and Löve(1958) have pointed out that there are three stages in the development of taxonomy: the explorative phase, the systematic phase, and the biosystematic phase. At present taxonomic work in western Canada is largely confined to stages one and two. The taxa are well documented and data on regional and local variation are available. In the present study, work on the genus Betula in western Canada has reached the biosystematic phase.

Because of the basic differences between the fact-finding phase of taxonomy and the codification of the results of this fact-finding phase, the two sections are often separated. This policy has become common practice in recent years (Horton, 1963; Anderson, 1964; Wiens, 1964).

The present study was undertaken to clarify the taxonomy of the genus Betula in western Canada. The data are separated into two parts, the first a formal codification of information, and the second a systematic section. Before this study was undertaken, the problems caused by variation and hybridization in the birches were evident. Therefore, several systematic and biosystematic techniques have been applied to the birches in order to obtain as much information as possible upon which to base conclusions.

Biosystematics provides techniques for the systematic phase of taxonomy. In section II techniques of biosystematics have been applied, since in genera containing critical species, morphological taxonomic methods are inadequate to explain relationships, and it is necessary to use as many methods and characters as possible to elucidate the problems. Some of these are introduced below.

Chromosome numbers and chromosome morphology are useful additional morphological characters which are used today in many taxonomic investigations. The importance of polyploidy in species origin and chromosome number as a morphological character make such studies extremely

important in the study of relationships between taxa.

Experimental methods have been applied to the study of relationships between taxa by many workers (Turesson, 1922; Clausen, Keck and Hiesey, 1939, 1940, 1941, 1951; Blakeslee, 1945) and the influence of ecological factors has also been studied. Experimental cultivation was used by Turesson to show differentiation of a population into different genetical assemblages adapted to environments. These he called ecotypes. Using data obtained from these and other studies, many biosystematic categories have been proposed based on the experimental analysis of populations (Turesson, 1922, 1922a; Gregor, 1942, 1944; Danser, 1929; Baker, 1952).

Hybridization studies have been made on plant populations by many workers (Anderson, 1936, 1941, 1948, 1949, 1954; Stebbins, 1956; Hall, 1952; Grant, 1953; Heiser, 1949, 1951, 1961; Tucker and Haskell, 1960; Steele, 1961) and much insight has been gained into the relationships and nature of species through use of the results. Cytological studies are also extremely important in determining the hybrid origin of taxa (Johnsson, 1944, 1945, 1949; Woodworth, 1929, 1930, 1931). Statistical methods have been increasingly applied, and new methods have been devised to make the data gathered more meaningful (Anderson, 1941, 1949; Stebbins, 1950).

Various chromatographic methods have been applied

to plant taxa, and a certain amount of information can be obtained regarding relationships between them. Paper chromatography (Smith and Levin, 1963; Alston and Turner, 1962, 1963; Stebbins, *et al*, 1963; Geissman, 1962) has come into increasing usage in the last few years.

Certain information provided by other techniques such as serological studies, experimental plots, and electron microscopy have also been applied to taxonomy, although these were not within the range of the present investigation.

The thesis is divided into two parts. The first part is a codification of information on *Betula*, *i*.*e*., name, synonyms and descriptions which have been developed in part as a result of conclusions from the biosystematic section. The first part, which follows the introduction, begins with a description of the genus followed by keys to taxa. For each taxon the format is as follows:

1. Name
2. Synonymy
3. Description and types
4. Distribution
5. Brief taxonomic notes including lists of species with which the taxon hybridizes (with page references to details in the second part)
6. Citation of material examined

In the second section, the biosystematic materials and methods are discussed, followed by the seven hybrid populations in which the following sequence is observed:

1. Characters of gross morphology used in the analysis
2. Polygonal graphs
3. Hybrid index
4. Pictorial scatter diagrams
5. Various statistical analyses
6. Chromatographic data
7. Chromosome numbers
8. Discussion

Certain tables and figures are in the text, others (reference type) are in the appendix (designated by a small "a" prefixing the number).

LITERATURE REVIEW

The genus *Betula* consists of about 40 species of trees and shrubs widely scattered throughout the cooler regions of the northern hemisphere. According to Nuttall (1842) the name is supposedly derived from *Betu*, the Celtic name for birch. It was apparently adopted by the Romans (Sargent, 1896; Britton, 1908).

The genus is normally divided into two sections, *Betulaster* and *Eubetula* (Winkler, 1904). Prantl (1894) and others have divided it into four series, *Acuminatae*, *Costatae*, *Excelsae*, and *Humiles*. The following is the currently accepted classification of the genus (Rehder, 1949; Krüssmann, 1962):

Sections and Series of the Genus *Betula*

Sect. I. BETULASTER (Spach) Regel in De Candolle Prodr. 16,2: 179 (1868); Winkler in Engler, Pflanzenreich, IV. 61 (Heft 19): 88 (1904). *Betulaster* Spach in Ann. Sci. Nat. Bot. ser. 2, 16: 198 (1841). *Betula* subgen. *Betulaster* Endlicher, Gen. Pl. Suppl. 4: 20 (1847).

Ser. 1. ACUMINATAE Regel in Bull. Soc. Nat. Moscou, 38,2: 397 (1865) "sect"; in De Candolle, Prodr. 16,2: 179 (1868) "sect. *Betulaster* subsect. *Acuminatae*".

Sect. II. EUBETULA Regel in Nouv. Mem. Soc. Nat. Moscou, 13,2: 74 (Monog. Betul. 16) (1861); H. Winkler in Engler, Pflanzenreich, IV. 61 (Heft 19): 57 (1904).

Ser. 2. COSTATAE Regel in Bull. Soc. Nat. Moscou, 38,2: 412 (1865); in De Candolle, Prodr. 16,2: 175 (1868) "sect. *Eubetula* subsect. *Costatae*."

Betula sect. *Eubetula* subsect. *Lentae* Regel, *l.c.* (1868).

Ser. 3. EXCELSAE Koch, as *Betula* sect. I. *Excelsae* Koch, Syn Fl. Germ. Helv. ed. 2, 760 (1843).

Betula (Abth.) *Albae* Regel in Bull. Soc. Nat. Moscou, 38,2: 396 (1865).

Betula (Abth.) *Dahuricae* Regel, *l.c.* (1865).

Betula sect. *Eubetula* Reg. subsect. *Albae* Reg. ser. *Verrucosae* et ser. *Pubescentes* Rothmaler & Vasconcellow in Bol. Soc. Broter. Ser. 2, 14:145 (1940).

Ser. 4. HUMILES Koch, as Betula sect. Humiles Koch, Syn Fl. Germ. Helv. ed. 2, 2: 761 (1844); Prantl in Nat. Pflanzenfam. III. 1:45 (1887).

Chamaebetula Opiz in Lotos, 5: 158 (1855).

Apterocaryon Opiz, l.c. (1855).

Betula (sect.) Fruticosae Regel in Bull. Soc. Nat. Moscou, 38,2: 396 (1865).

Betula subsect. Nanae Regel in De Candolle, Prodr. 16,2: 162 (1868).

In the second section listed above a new series, Series Fontinalae, is described in this study (see page 25). Of the five series, four are represented in North America, and three in western Canada. The series Acuminatae has a rather restricted range in the Himalayas and Japan. The Costatae are represented in central and eastern Asia by Betula ermanii[1], B. utilis, B. albo-sinensis, B. costata, and others while in eastern North America the series is represented by B. nigra, B. lenta, and B. lutea. The series Excelsae is represented in eastern and central Asia, Europe and North America. B. verrucosa is common to both old world regions, while B. dahurica is in Asia, and B. pubescens is in Europe. In the new world, B. populifolia and B. papyrifera are found in the northeast and B. papyrifera, B. resinifera, and B. kenaica are western representatives.

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1. For names, synonyms, and reported chromosome numbers of listed birches, see Table a17.

The series Humiles, like the Excelsae, are more or less circumpolar, represented in North America by B. pumila, B. pumila var. glandulifera, B. glandulosa, and B. nana. The series Fontinalae is represented in North America by B. fontinalis.

About the origin of the genus and evolutionary relationships within it, very little is known. Abbe (1938) derives axillary complex of birch flowers from an ancestral form with cymose inflorescences, each composed of a median 3-flowered group and two lateral 3-flowered groups. With the new theory on the origin of the Angiosperm flower proposed by Melville (1962, 1963), a new interpretation of the flower is likely. In the light of Melville's theory the Betulaceae and its allies would appear to form a rather distinct evolutionary line that has probably existed for a very long time. It is known that the genus is at least 80,000,000 years old because birch fossils have been found in the Cretaceous (Prantl, 1894; Chaney, 1940, 1947). Fossil leaves have been found from the Miocene of Iceland (Lindquist, 1947) and these are identified as Betula callosa, a modern taxon.

With regard to the origin of series, Vasil'ev (1958) suggests that except for central Asiatic species (presumably the Acuminatae), the Costatae, Excelsae, and Humiles arose from a Costatae-type ancestor. It was further suggested by Vasil'ev that the region in which this occurred was the

Baikal-Sayan area, U.S.S.R. and that the Excelsae group at least, originated in the late Pliocene or Pleistocene. From this center of origin, the birches have spread east and west to occupy their present positions in Europe and North America. In the absence of any of the evidence for Vasil'ev's suggestions, an evaluation is not possible, but it does not seem likely that the divergence took place as late as the Pliocene or Pleistocene because of the presence of birches referrable to modern series in the early Tertiary flora.

Of interest here may be the suggestion by several early workers recently reiterated by Sporne (1956, 1959) and Thorne (1958) that ontogenetical relationships may be of value in suggesting phylogeny. Sporne (1956) among others has said that seedlings often show ancestral characters that are missing from mature plants, and in this respect the juvenile foliage of series Humiles may be significant (see Figure al). In Betula papyrifera and B. resinifera (Excelsae), and B. fontinalis (Fontinalae), the juvenile foliage is very similar in shape and margin of leaf to mature foliage, while in the Humiles there is dimorphism, that is, the juvenile foliage is similar to that of series Excelsae and series Fontinalae, while there is no such similarity in mature foliage. It is therefore possible that the series Humiles is a more recently evolved member of the genus. In this connection it is to be noted that they occupy habitats with arctic characteristics and

these are perhaps amongst the most recently developed in the Northern Hemisphere (Johnson and Packer, 1964, unpublished).

Taxonomic History of the Genus Betula in North America

Prior to 1838, when Hooker published his Flora Boreali-Americana, very few studies of the birches had been made. Linnaeus (1753) described two American species, Betula lenta and B. nigra, as well as two European species, B. alba and B. nana. Marshall (1785) described B. papyrifera from North America and Michaux (1803) discussed B. papyrifera, with particular regard to its economic importance. Hooker (1838) listed with descriptions eight species of Betula; B. occidentalis, B. populifolia, B. papyracea, B. excelsa, B. lenta, B. pumila, B. glandulosa and B. nana, of which one, B. occidentalis was a new species. In his North American Sylva, Nuttall (1842) listed six species of birch: B. occidentalis, B. rhombifolia, B. glandulosa, B. papyracea, B. populifolia, and perhaps B. fruticosa. He described only two of these, B. occidentalis and B. rhombifolia. Regel (1861, 1865, 1868) listed and described many North American species of Betula. He also listed many subspecies, varieties, and forms; many of which are not easily distinguishable. Lyall (1864) described the botanical collections made in northwestern America and included B. occidentalis Hook., "a tree growing to the height of 60 or 70 feet, and most common about the borders of the forest". In 1880,

Watson in Geological Survey of California Botany Vol. II listed and described two species, B. occidentalis Hook. and B. glandulosa Michx. Sargent in his Silva of North America (1896) listed and described six tree birches of North America, and in his Manual of the Trees of North America (1905) he listed nine arborescent species, among which he included B. fontinalis which is a large shrub and B. eastwoodae, also a shrub.

Fernald (1902) combined North American and European species, justifying this by the apparent similarities in descriptions and comparative studies in which he used only a limited amount of herbarium material. He established the following complexes using a "super-species" or "Rassenkreis" system: B. verrucosa-like forms in which was included such species as B. kenaica, North America; B. resinifera, North America; B. alba subsp. verrucosa, North America and Asia; B. japonica, Asia. Another complex was the B. pubescens-like forms, including B. papyrifera, North America and B. alba and B. pubescens, Eurasia. However, in 1945 Fernald revised his opinion in a study of the birches of eastern North America and repudiated his earlier work, commenting that conservative treatments were often as "far afield as those that split beyond the normal divergencies in Nature." In this treatment Fernald suggested that most of the North American species are endemic.

Britton (1908) in his North American Trees listed and described 15 arborescent species, among which were included several which have been considered varieties of *B. papyrifera*, and several of which are of hybrid origin (*B. utahensis*, *B. sandbergii* and possibly *B. alleghaniensis*).

In 1909 Butler described the western North American birches. He recognized 17 species, many of which were new, and several of which have since been shown to be of hybrid origin. He thought that many of the confusing varieties and hybrids had been proposed on the basis of a few superficial characters and without understanding of living material or habitat and distribution. It is easy to understand the difficulties that Butler mentioned, but it seems doubtful that these are solved by calling all of the taxa species.

The polymorphism of the species in the genus *Betula* is due at least in part, to the extensive occurrence of hybridization. Several supposed hybrids had been described in the early 1900's: *B.* x *sandbergii*, described as a hybrid between *B. pumila* var. *glandulifera* and *B. papyrifera* by Rosendahl (1916, 1928); *B.* x *jackii*, described as a hybrid between *B. pumila* and *B. lenta* by J. G. Jack (1895); *B.* x *purpusii*, a hybrid between *B. lutea* and *B. pumila* var. *glandulifera* (Rosendahl, 1928); and *B.* x *conmixta*, suggested by Sargent (1922) to be a hybrid between *B. alaskana* (*B. resinifera*) and *B. glandulosa*. Winkler (1904)

described eight natural Betula hybrids and listed six others. Those which have not already been mentioned are the following: B. pubescens x B. nana (B. x intermedia); B. verrucosa x B. humilis; B. pubescens x B. humilis; B. pubescens x B. verrucosa (B. x aurata); B. nana x B. verrucosa (B. x fennica); B. populifolia x B. papyrifera; B. davurica x B. lenta; B. pumila x B. nana; B. pumila x B. glandulosa; B. verrucosa x B. papyrifera (B. x koehnei) and B. coerulea-grandis x B. populifolia (B. x coerulea).

Recent Taxonomic Studies in Europe and North America

In studies of the taxonomy of Betula in recent years, the Europeans have been most active. Many investigations have been undertaken on relationships within the genus, and also on hybridization in which Betula pubescens and B. verrucosa and their varieties have been most commonly used.

In the detailed taxonomic studies of European birches, the same varied approach by the investigators occurs as has been noted above in North American studies. For example, Kindberg (1909) in a study of the Scandinavian tree birches established 22 species of equal rank. Gunnarsson (1925), however, recognized only five species but regarded nearly every tree as a hybrid between two or more species. Taxa of lower rank, usually varieties, have been recognized by other authors, particularly Lindquist (1947).

Lindquist (1947) has suggested that the chromosome number 2n = 56 is usual in _Excelsae_, which is incorrect since the common number in all _Betula verrucosa_-like groups is 2n = 28, and the numbers which are common in _B. papyrifera_ are 2n = 70 or 84.

Woodworth (1931) published a series of _Betula papyrifera_ chromosome numbers which show an elegant method of separating at least some _B. papyrifera_ varieties:

B. papyrifera var. _cordifolia_	2n = 56
B. papyrifera var. _subcordata_	2n = 56
B. papyrifera	2n = 70
B. papyrifera var. _kenaica_	2n = 70
B. papyrifera var. _occidentalis_	2n = 84

However, 2n = 84 is not restricted to _B. papyrifera_ var. _occidentalis_ (_B. papyrifera_ var. _commutata_) but occurs as one of a series of numbers between 70 and 84 in the whole _B. papyrifera_ complex. The inclusion of _B. papyrifera_ forms with dark bark from Masschusetts in _B. papyrifera_ var. _commutata_ is considered by Johnsson (1949) to be a mistake, since it is believed that these are most likely just color variations, and perhaps have no relationship to _B. papyrifera_ var. _occidentalis_, which will be discussed in the present study.

Johnsson concluded that _B. papyrifera_ forms are different from _B. pubescens_ forms which have 2n = 56. He suggested that a comparison of _B. papyrifera_ var.

subcordata with a chromosome number of 2n = 56 according to Woodworth (1931) and B. papyrifera var. cordifolia (2n = 56, Woodworth, 1931) with B. pubescens would be interesting. The B. papyrifera var. subcordata portion of this problem has been at least partially elucidated in the present study.

The kinship between B. verrucosa and B. japonica (that is, between European and Asiatic B. verrucosa-like forms) is shown by Johnsson (1945) in that the hybrid of these two has a chromosome number of n = 14 and regular meiosis. Some recent taxonomists have followed Fernald (1902) in considering the Asiatic B. japonica (syn. B. platyphylla) closely related to the Alaskan B. resinifera and B. kenaica (Johnsson, 1949). However, Hultén (1944) states that B. kenaica is more closely related to B. japonica than it is to B. resinifera, and possibly is a race of B. japonica. However, B. japonica has a chromosome number of 28 while the chromosome number of B. kenaica (B. papyrifera var. kenaica) has been determined by Woodworth (1931) to be 2n = 70, which probably indicates that B. kenaica is not as closely related to B. japonica as Hultén supposes.

Johnsson (1949) in his comparison of the North American, European, and Asiatic Betula verrucosa-type birches included B. fontinalis in this complex. He therefore implies a close relationship between B. fonti-

nalis and the B. verrucosa-like birches, which seems highly unlikely on the basis of morphology. A chromosome number of $2n = 28$ has been published by Woodworth (1931) for B. fontinalis var. piperi. The chromosome number of typical B. fontinalis is also $2n = 28$. It was suggested by Johnsson (1949) that the eastern American equivalent of B. fontinalis is B. populifolia which does not seem to be likely on the basis of morphology.

Several of the investigators worked on hybridization within the genus Betula. Gunnarson (1925) considered many of the birches in Scandinavia to be the result of protracted hybridization. Helms and Jorgensen (1925) also studied hybrids in Scandinavia, and included some chromosomal studies in their investigation. In 1929, 1930, and 1931, Woodworth reported cytological investigations of several birch species and hybrids. He suggested that several birches were of hybrid origin on the basis of their meiotic irregularities. In hybrid birches that are the result of crosses between taxa of like chromosome numbers, meiotic irregularities were not common.

Lindquist (1947) and Johnsson (1944, 1945, 1949) have recognized the two large complexes, B. pubescens-like forms and B. verrucosa-like forms in a way very similar to that of Fernald (1902). In 1944 and 1945, Johnsson reported some experimental results of artificial

hybridization in the genus *Betula* with an analysis of *B. verrucosa* crosses and *B. pubescens* crosses. This investigator found that while *Betula* species within the series *Excelsae* crossed with rather high fertility, crosses between the two series, *Excelsae* and *Costatae*, produced very few F_1 plants. There also seemed to be a reduction in germination of hybrids between *B. verrucosa* and *B. pubescens* (both members of *Excelsae*). Johnsson believed that the series limit represents a very effective sterility barrier between *Excelsae* and *Costatae* (*B. pubescens* crossed with each of the following: *B. ermanii*, *B. albo-sinensis*, *B. lenta*, and *B. lutea*) (Johnsson, 1949). However, an equally effective sterility barrier was found by Johnsson between *B. verrucosa* and *B. pubescens*. The intermediate forms between these two have been, in the past, considered hybrids (Regel, 1865; Morgenthaler, 1915; Helms and Jorgensen, 1927) but Johnsson has shown that artificial hybrids between them are difficult to produce, at least with the chromosome number of 2n = 42 that was reported by Helms and Jorgensen (1927). Johnsson found the most common number of the hybrid to be 2n = 56. This worker has shown that the sterility barrier that separates *B. verrucosa* and *B. pubescens* cannot be explained on the basis of a difference in chromosome number since crosses between these two species and the

84 chromosome _B. papyrifera_ are relatively fertile.

Certain crosses between series _Excelsae_ and _Costatae_ have been made, although they are mostly sterile (Johnsson, 1945). In addition to the above, Smith and Nichols (1941) have reported artificial crosses of _Excelsae_ and _Costatae_: _B. japonica_ x _B. lenta_; _B. populifolia_ x _B. lenta_; _B. japonica_ x _B. nigra_. Crosses of _B. verrucosa_ x _B. maximowicziana_ (_Excelsae_ x _Acuminatae_) have been made (Johnsson, 1949) and Smith and Nichols (1941) have reported _B. japonica_ x _B. maximowicziana_ (_Excelsae_ x _Acuminatae_) has been successful. No attempts have been made using species belonging to series _Humiles_, but spontaneous hybrid individuals are found between _B. nana_ and two _Excelsae_ species, _B. verrucosa_ and _B. pubescens_. Hybrids between _B. glandulifera_ (_Humiles_) on one hand and _B. papyrifera_ (_Excelsae_) and _B. lutea_ (_Costatae_) on the other, are described by Rosendahl (1916, 1928) and Woodworth (1929, 1930), who also mentioned _B. lenta_ x _B. pumila_ (_Costatae_ x _Humiles_). Additional hybrids between _Excelsae_ and _Humiles_ were listed by Krüssmann (1962): _B. papyrifera_ x _B. pumila_ (_B._ x _borggreveana_) and _B. nana_ x _B. papyrifera_ (_B._ x _hornei_).

Johnsson (1949) has shown that the _Betula verrucosa_ x _B. papyrifera_ hybrid has a regular meiosis with 28 bivalents and 2n = 56. He suggested that this hybrid may be the origin of one of the 56 chromosome varieties

of *B. papyrifera*. A similar situation, the hybridization of *B. resinifera* x *B. papyrifera* is discussed in the present study. The result of this cross is often 2n = 56. Another large proportion of the 2n = 56 birches have an entirely different origin, resulting from a *B. fontinalis* x *B. papyrifera* hybrid (page 103). These entities have, to a certain extent, been erroneously combined in the western variety *B. papyrifera* var. *subcordata*.

Löve and Löve (1956) have published a cytotaxonomic study of Icelandic birches, along with an analysis of present birch flora. They have concluded that widespread introgression has taken place between at least six taxa of octoploid *Betula* usually listed as separate species. They state that this introgression has been going on for a long time, and it has wiped out the limits between some of the taxa almost entirely.

Several birch hybrids have been studied using various types of population analysis. Froiland (1952), in his analysis of *Betula* x *andrewsii* determined that this taxon was a hybrid between *B. fontinalis* and *B. papyrifera* and that introgression was in the direction of *B. papyrifera*. In 1959 Natho studied relationships and hybridization in four species, *Betula humilis*, *B. pendula*, *B. pubescens* and *B. carpatica*. He found *B. pendula* and *B. pubescens* were introgressed by *B. humilis*. Extensive studies have been made of *B.* x *sandbergii*

(*B*. *pumila* var. *glandulifera* x *B*. *papyrifera*) (Rosendahl, 1916, 1928; Clausen, 1959, 1962, 1963). Clausen has concluded that gene flow is in the direction of *Betula papyrifera*.

As can be seen by the above, various approaches to the species problem in *Betula* have been adopted. The widely divergent proposals of Butler (1909) or Fernald (1902) may be regarded as correct by some taxonomists, but, as a result of the present studies, neither is thought to be very satisfactory, and an intermediate position is adopted. In certain cases the genus is more natural than the species within it (Stebbins, 1950) and in these genera there are apt to be widely divergent views on the nature of the species within them. An example is the genus *Betula*. However, even in genera of this type, it is possible to recognize different morphological types which have different geographical distributions, and these can be recognized as species. From a purely practical point of view, it is preferable not to follow Fernald because many of the taxonomic problems may be overlooked when they are submerged in such large species complexes, but on the other hand, it is not a sound procedure to follow Butler in considering each morphological variant as a species, thus disregarding normal population variation and the effects of hybridization. In the present study, certain taxa are considered

species in the classical sense because there are morphological, ecological and geographical differences between them, and they have maintained themselves in nature as interbreeding populations.

However, results of interspecific hybridization are the swarms of variants found in such genera as Salix, Betula, Quercus, Rubus, and Carex (Drury, 1956), the classification of which has led to confusion when based solely on morphological concepts. In these genera, species preserve their identity in the face of continued and widespread hybridization with neighboring species, and the whole complex must not be considered as one species.

Using modern biosystematic techniques, hybridization between several of the species in the genus Betula has been shown to occur. Prior to the Pleistocene, these birches may have been distinct morphologically, ecologically, and geographically, though perhaps they never were. Internal isolating mechanisms perhaps never existed in them. Despite reports by Johnsson of reproductive barriers in certain European birches, it is possible that a situation similar to that proposed by Rattenbury (1962) to explain hybridization in New Zealand exists in the genus Betula in western Canada, and that there is selection for lack of internal isolation. Plants are long-lived, and a hybrid, once formed, has the opportunity for

recombination, thus increasing the probability that a fertile type capable of perpetuating itself will arise. The result of lack of internal isolating mechanisms means that the application of a rigorous species concept based on crossing ability is impossible. From the above we can see that where ever they have been studied there are problems in the *Betula* taxonomy.

The present work was undertaken to elucidate the problems in the genus *Betula* in western North America. In pursuing this objective over 1000 collections were made in Alberta and British Columbia during the summers of 1961-1963. One set of all collections and the type specimens of new hybrid taxa are deposited in the University of Alberta Herbarium (ALTA), Edmonton. In addition, studies have been based on herbarium material obtained from: National Museum of Canada, Ottawa (CAN); Botany and Plant Pathology Division, Department of Agriculture, Ottawa (DAO); New York Botanic Garden (NY); Gray Herbarium, Harvard University (GH); Arnold Arboretum, Harvard University (A); University of Minnesota, Minneapolis (MIN); University of Colorado, Boulder, (COLO); U. S. National Museum (Department of Botany), Smithsonian Institution, Washington, D. C. (US); The W. P. Fraser Memorial Herbarium, Department of Plant Ecology, University of Saskatchewan, Saskatoon (SASK).

BETULA Linnaeus, Sp. Pl. 982 (1753)

Gen. Pl. 422, no. 933 (1754); Regel in Nouv. Mem. Soc. Nat. Moscou, 13,2: 67-131, T. 4-13 (Monog. Betul. 9-73, 1861); in De Candolle, Prodr. 16, 2: 162-180 (1868).

Lectotype: B. verrucosa Ehrh.

Deciduous trees or shrubs; the bark often exfoliating; branchlets often dotted with resinous glands. Buds sessile, elongate, with numerous ovate, acute scales. Leaves alternate, crenate to serrate; stipule ovate and acute or oblong-obovate, scarious, caducous. Flowers monoecious, in catkins. Staminate catkins cylindrical, elongate, pendulous, solitary or clustered, appearing in summer or autumn in the axils of the last leaves of a branchlet or near the ends of short lateral branchlets; each bract subtending 3 flowers and 2 bractlets; staminate flower of minute perianth and 2 stamens which are bifid below the anthers; pollen 3-pored. Pistillate catkins ovoid to cylindric, terminal on the short spur-like lateral branchlets; the bracts 3-lobed and eventually deciduous, each bract bearing 2 or 3 flowers; pistillate flower a naked pistil, without bractlets or perianth. Fruit a samara, the ovate or obovate body bearing 2 membranous lateral wings and terminated by 2 short persistent styles. Endosperm absent; wind pollinated.

Ser. 1. ACUMINATAE Regel

Fruiting catkins cylindrical, pendant, clustered or single, 4-11 cm long, samara wings somewhat broader than the body, leaves 7-14 cm long.

Ser. 2. COSTATAE Regel

Fruiting catkins single, 2-5 cm long, samara wings not, or barely broader than the body.

Ser. 3. EXCELSAE Koch

Mostly trees, rarely shrubs; samara wings broader than the body.

Ser. 4. HUMILES Koch

Shrubs; leaves with 2-5 nerve-pairs, samara wings narrower than the body.

Ser. 5. FONTINALAE n.ser.

Frutica magna cum fusco non-exfolianti cortice; folia 2-5 cm longa, habentia 5-7 pares lateralium venarum in foliis; alae samerarum non angustiores quam corpus.

Large shrubs, with brown non-exfoliating bark; leaves 2-5 cm long, having 5-7 pairs of lateral leaf veins; samara wings as broad as the body.

KEY TO NON-HYBRID BIRCH TAXA IN WESTERN CANADA[2]

a. Trees with exfoliating bark, brown to white; samara wings broader than body.

  b. Leaves acuminate, deltate to trullate, not pubescent in the axils below; branchlets glandular resinous.

  Betula resinifera p. 61

  b. Leaves acute to acuminate, ovate, pubescent in the axils below; branchlets not glandular resinous.

  Betula papyrifera p. 75

a. Shrubs with non-exfoliating bark, yellow-brown to brown; samara wings not broader than body.

  c. Shrubs with shiny bark; leaves serrate to doubly-serrate; branchlets with reddish glands; samara wing as broad as body.

  Betula fontinalis p. 30

  c. Shrubs with dull bark; leaves crenate to crenate-serrate; branchlets with yellow to white glands; samara wing narrower than body.

    d. Leaves obovate; branchlets sparsely yellowish glandular; samara wing equals ½ body width; leaf margin with more than 10 crenations.

    Betula pumila var. *glandulifera* p. 51

    d. Leaves round; branchlets densely white glandular; samara wing less than ½ body width; leaf margin with less than 10 crenations.

    Betula glandulosa p. 41

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2. If this key is used, it is often found that it is impossible to arrive at a taxon. In this case it is probable that the birch is of hybrid origin, and the second key should be used. The keys have been tested by several individuals and seem to be satisfactory.

KEY TO WESTERN CANADIAN BIRCH TAXA, INCLUDING HYBRIDS

a. Trees with exfoliating bark, brown to white; samara wings broader than body.

b. Leaves deltate to trullate, acuminate, not pubescent in vein axils beneath; branchlets usually glandular resinous, not in Rocky Mountains.

Betula resinifera p. 61

b. Leaves ovate, acute to short acuminate, often pubescent in vein axils beneath; branchlets usually not glandular resinous, often pubescent.

c. Leaves more than 5 cm long, with more than 7 pairs of lateral leaf veins.

d. Leaves more than 6 cm long, with 8 or more pairs of lateral leaf veins, and 30-40 serrations on each leaf margin.

Betula papyrifera p. 75

d. Leaves less than 6 cm long, with 7 pairs of lateral leaf veins, and 25-35 serrations on each leaf margin, not in Rocky Mountains.

Betula x winteri p. 109

c. Leaves less than 4 cm long, with less than 7 pairs of lateral leaf veins.

e. Leaves broadly ovate; bark usually gray to gold, not in bogs.

Betula x utahensis p. 101

e. Leaves elliptic to ovate, bark usually yellow to white, bogs.

Betula x sandbergii p. 113

a. Shrubs with non-exfoliating bark, yellow-brown to brown; samara wings not broader than body.

f. Branchlets not glandular.

g. Fruiting catkins about 1.5 cm long; not in bogs; rare.

Betula x arbuscula p. 107

g. Fruiting catkins 2-2.5 cm long; bogs.

Betula x sandbergii p. 113

f. Branchlets glandular.

h. Large shrubs with shining bark; leaves serrate to doubly serrate; branchlets with reddish glands.

i. Bark brown or red-brown, glands dense; leaves with 20-25 serrations along one margin.

Betula fontinalis p. 30

i. Bark yellow-brown, rarely lighter, glands sparse, leaves with 25-40 serrations along one margin.

Betula x utahensis p. 101

h. Small shrubs, with dull bark; leaves crenate to crenate-serrate, branchlets with yellow to white glands.

j. Leaves round, crenate, usually with less than 10 crenations on one leaf margin, normally with 3-4 pairs of lateral leaf veins; wings of samara less than ½ width of body.

Betula glandulosa p. 41

j. Leaves elliptic, ovate to obovate, crenate to crenate-serrate, usually with more than 10 crenations on one leaf margin, normally with more than 4 pairs of lateral leaf veins, wing of samara equal to or greater than ½ body.

k. Leaves elliptic to obovate, usually crenate, with 10-20 crenations on one leaf margin; branchlets with scattered yellow-white glands.

l. Leaves elliptic, 2-2.5 cm long, crenate, usually 10-15 crenations on one leaf margin; branchlets with scattered yellow-white glands, wing equal to ½ width of body.

Betula x sargentii p. 92

l. Leaves obovate, 2-4 cm long, crenate to crenate-serrate, usually 14-20 crenations on one leaf margin, branchlets with sparse yellow glands; wing more than ½ width of body.

Betula pumila var. glandulifera p. 51

k. Leaves broadly ovate, usually crenate-serrate, with 15-25 crenations on one leaf margin; branchlets with yellow glands.

m. Leaves 2-4 cm long, petiole 5-10 mm long; body of samara wider than wing; Rocky Mountains and northern Canada.

Betula x eastwoodae p. 97

m. Leaves 3-5 cm long, petiole 10-15 mm long; body of samara equals wing; bogs of interior Alberta and northward, not in Rocky Mountains.

Betula x uliginosa p. 89

<u>BETULA</u> <u>FONTINALIS</u> Sargent, Bot. Gaz. 31:237-239 (1901) Man. Trees N. Am. 207, fig. 174 (1905); Jour. Arnold Arb. 1:64 (1919); Man. Trees N. Am. Vol. I 218, fig. 206 (1922); Rydberg, Flora of Colorado 96 (1906); Flora of the Prairies and Plains of Central North America 260 (1932); Britton, North American Trees 253 (1908); Butler, Bull. Torrey Bot. Club 36:430 (1909); Abrams, Illustrated Flora of the Pacific States Vol. I 512 (1940); Clements and Clements, Rocky Mountain Flowers 221 (1945).

<u>B</u>. <u>occidentalis</u> Hooker, Fl. Bor. - Am. ii. 155 (1838) <u>nom</u>. <u>confus</u>. (Art. 69 and 70, Int. Code of Bot. Nomen.), in part, as to Douglas and Drummond specimens and part of description; Nuttall, N. Am. Sylva Vol. 1:23 (1842); Watson, Botany Vol. II, Geol. Surv. of Calif. 80 (1880); Sargent, Silva N. Am. 9:65, t. 453 (1895) in part; Rydberg, Flora of Montana and the Yellowstone National Park 116 (1900); Howell, Flora of Northwest America Vol. I, 613 (1903); Fernald, Rhodora 47:314 (1945); Raup, Sargentia VI: 163 (1947); Porsild, National Museum of Canada Bull. No. 121:153 (1951), in part; Davis, Flora of Idaho 236 (1952); Harrington, Manual of the Plants of Colorado 180 (1954); Breitung, Am. Midland Nat. 58:25 (1957); Moss, Flora of Alberta 185 (1959); Krüssmann, Handbuch der Laubgehölze, 235 (1962).

<u>B</u>. <u>rhombifolia</u> Nuttall, N. Am. Sylv. 1:24, t. 8 (1842), in part, not Tausch (1838).

B. microphylla var. *fontinalis* M. E. Jones, Contrib. West. Bot. 12:77 (1908).

B. microphylla sensu Raup, Contrib. Arnold Arb. VI:152 (1934); Jour. Arnold Arb. 17:242 (1936); Porsild, Sargentia 4:29 (1943), not Bunge (1835).

B. papyrifera subsp. *occidentalis* (Hooker) Hultén, Fl. Alaska and Yukon 4:582 (1944), in part.

B. glandulosa x *resinifera* Hultén, Fl. Alaska and Yukon 4: 575 (1944) in part.

Large thicket-forming shrub, 1-10 m tall, usually several trunks present, up to 4 dm in diameter, branches ascending, spreading, somewhat pendulous, forming a broad open head; branchlets slender, at first appearance light green, glabrous or puberulent and covered with persistent, lustrous, reddish, resinous glands which darken to a red-brown in the first winter. Bark not readily exfoliating, dark bronze to brown, often very lustrous, marked by pale brown longitudinal lenticels. Winter-buds ovoid, acute, very resinous, chestnut-brown, 2-3 mm long. Leaves broadly ovate, acute, sharply and often doubly-serrate, except at the truncate to rounded or cuneate base, pale green and covered by conspicuous resinous glands when young, turning dull yellow in autumn, at maturity thin and firm, rather lustrous and glandular dotted, with multicellular, peltate glands on the upper surface and scattered safranin absorbing hairs on the epidermis, 2-5 cm long, 1-4 cm wide, with a slender pale midrib, glandular veins

and rather conspicuous reticulate veinlets; stomata averaging from 25-30 μ; petioles stout, glandular dotted, flattened on the upper surface, often flushed with red, 1-2 cm long; stipules broadly ovate, acute or rounded at apex, slightly ciliate, bright green, soon becoming pale and scarious. Staminate catkins 1-3, clustered, 1-3 cm long during the winter elongating to 4-5 cm in spring, bracts ovate, acute, light chestnut-brown, pale and ciliate on the margins, becoming apiculate at maturity; pollen averaging from 24-26 μ in diameter. Pistillate catkins short-stalked, about 15 mm long in flower, in fruit cylindric, rather obtuse, 20-30 mm long, 8-15 mm wide, erect or pendulous on slender glandular peduncles, 5-15 mm long; their bracts ciliate, puberulent or nearly glabrous, the lateral lobes ascending, shorter than the middle lobe. Fruit a samara, body 2-3 mm long, 1-2 mm wide, ovate or obovate, puberulent at apex, nearly as wide as its wing. Chromosome number 2n = 28.

Types: Holotype: Manitou Springs, Colorado, G. Engelmann and C. S. Sargent, June 21, 1880 (A). (See Plate a2).

Paratypes: Along Hatwai Creek, Nez Perces Co., Idaho, J. H. Sandberg, D. T. MacDougal, J. B. Leiberg, No. 33, April 24, 1892 (young specimen) (A); Manitou, Colorado, C. S. Sargent, August 19, 1894 (A).

Distribution: Moist locations near the banks of streams, lakes and marshes; often in mountain canyons to 10,000' in the Colorado Rocky Mountains, and to 5500' in the Canadian Rocky Mountains; British Columbia, Alberta, Saskatchewan, and Manitoba;

north in the Mackenzie District of Northwest Territories, throughout the Yukon, west into Alaska; south through Washington and Oregon to northern California (Sierra Nevada) and along the Rocky Mountains to Colorado, northern New Mexico and Arizona; east to northwestern Nebraska, the Black Hills of South Dakota and western North Dakota. See Figure 1.

Taxonomic Notes: Betula fontinalis hybridizes with: B. glandulosa (B. x eastwoodae); see page 97, 172, and B. papyrifera (B. x utahensis); see page 101, 185.

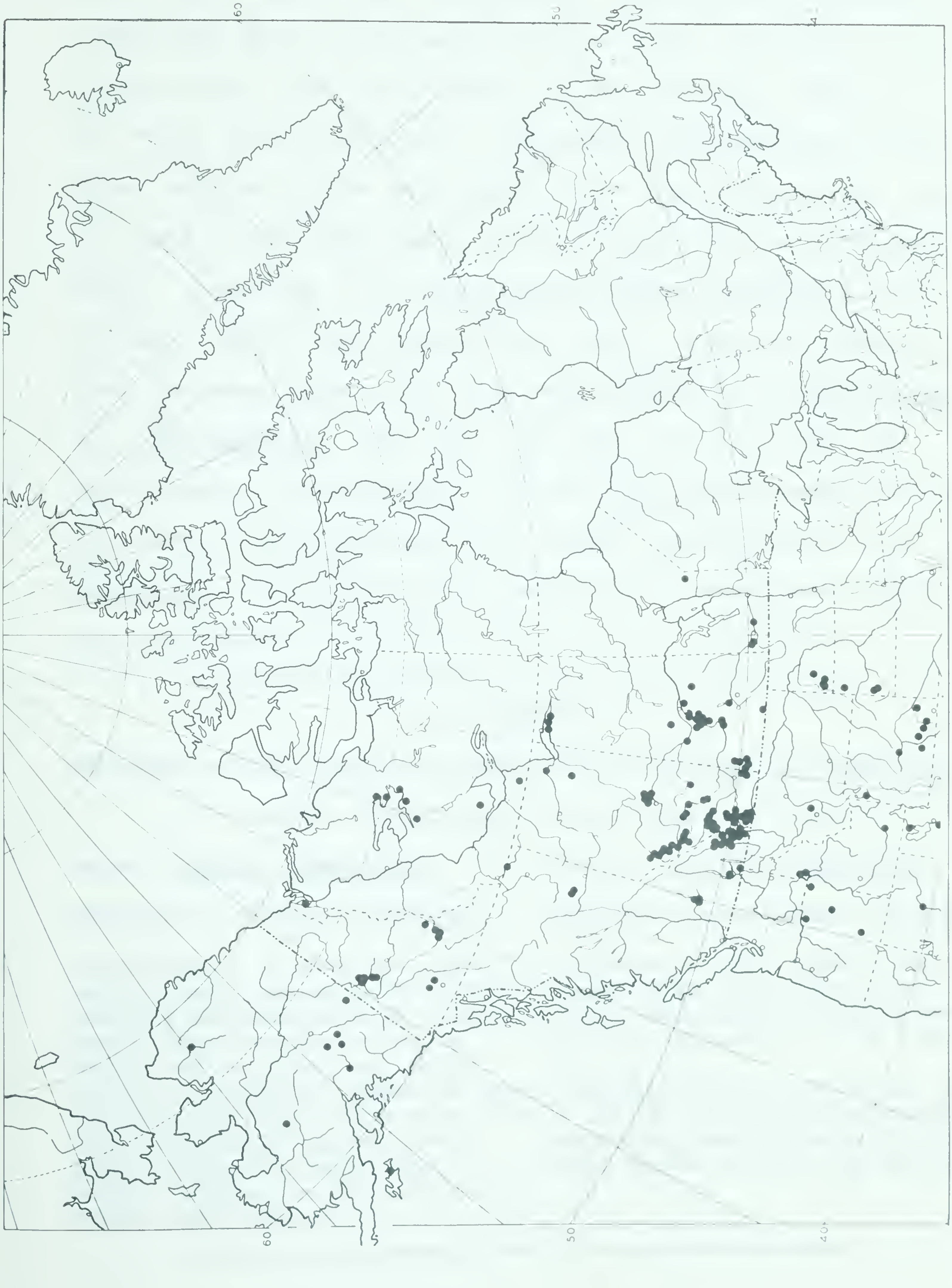
Hultén in his Flora of Alaska and the Yukon (1944) considered B. fontinalis under the heading B. glandulosa x B. resinifera and not as a distinct species. Under this heading he also erroneously included other hybrids, for example B. x eastwoodae and B. x utahensis. Hultén has concluded that B. fontinalis, B. x eastwoodae and B. x utahensis are part of a hybrid population of B. glandulosa x resinifera.

There has been much discussion in the literature (Sargent, 1902, 1905; Fernald, 1902, 1945) about the nomenclature, types, descriptions, etc. of Betula fontinalis and B. occidentalis. From a careful study of the specimens available, the original descriptions, and the comments made by the various workers, it must be concluded that B. occidentalis Hook. is an illegitimate name and must be rejected because both the description and the specimens listed with the original description are mixed (International Code of Botanical Nomenclature, 1961, Articles 69 and 70). Sargent

FIGURE 1

Distribution of *Betula fontinalis*.

(in N.W. North America)



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(1905) has stated that the original description of Hooker (1838) was drawn principally from material collected by Dr. John Scouler along the Straits of Juan de Fuca, which was the first listed specimen. The other two specimens listed, "Near springs on the west side of the Rocky Mountains. Douglas; and on the east side, from the mountains to Edmonton House. Drummond.", are apparently Betula fontinalis Sarg. Fernald (1945) felt that Sargent was in error in assuming that the description and type were applied to B. papyrifera var. occidentalis, the tall tree from the west coast of North America, and thought that the description applied vividly to the half-shrubby form that Sargent had described as B. fontinalis. The results of the writer's comparisons can be seen in Table 1.

TABLE 1.

Portions of the original description of Betula occidentalis Hooker which apply to two distinct taxa.

Tree: Betula papyrifera	Shrub: Betula fontinalis
Holotype - Scouler specimen	Douglas and Drummond specimens
"Petioles ½ to ¾ of an inch long, adult leaves 2-2½ inches broadly ovato-rhomboid, rather acute than acuminate, of a harsh and dry but not thick texture, slightly lobed at the margin, and incise-serrate, the serratures coarse and sharp, paler beneath, but never, either in the old or young state dotted."	"forming a low, small brushwood, 6-10 feet high, and never exceeding a few inches in the diameter of its trunk." "clothed with a red-brown bark, a little inclining to purple, copiously sprinkled with resinous warts in all the specimens"

In the writer's opinion there are several rather significant parts of the description which show that Hooker was referring to two different entities and combining them: 1) Both taxa are present among the listed representative specimens, of which the first listed, the holotype, is Betula papyrifera; 2) Two portions of the description apply only to B. fontinalis, "low small brush-wood" (although the measurements are somewhat small) and "copiously sprinkled with resinous warts in all specimens"; and 3) Two portions of the description apply only to B. papyrifera, "adult leaves 2-2½ inches," and "but (leaves) never, either in the old or young state dotted."

There is considerable variation in the glandular condition of Betula fontinalis and it would appear to be correlated with habitat conditions. Specimens collected in dry localities are often much less glandular than those from moist habitats. Certain collections from different habitats near Red Rock Canyon, Waterton National Park, show this variation. Collections from a marsh and stream bed (1645, 1646, 1647, 1648, 1649, 1650, 1676) are very resinous glandular while those from a dry wash (1673, 1674, 1675) are very much less so.

Representative specimens: BRITISH COLUMBIA: Golden City, Columbia Valley, J. Macoun, July 10, 1885 (CAN); Spence's Bridge, J. Macoun, June 3, 1889 (CAN); Peace River valley, Hudson Hope, H. M. Raup, E. C. Abbe, 3621 (CAN); Green Lake,

Cariboo, J. W. Eastham, 11537 (CAN); Bank Kootenay River, 17 miles N.E. of Kimberley, W. A. Weber, 2399 (CAN) (MIN); Trilobite point of interest, J.R.D., 2282, 2283, 2284, 2285, 2286, 2287 (ALTA); Thunder Hill campsite, Columbia Lake, J.R.D., 2290, 2292 (ALTA); Grande Prairie, July 20, 1900 (GH); Lost Lake, N. Victoria, C. F. Newcombe, Sept. 17, 1920 (A); North of Kimberley, A. Jablancry, 50-113 (DAO).

ALBERTA: Slough, Macleod, Dixon, 1761 (DAO); Banff, Butters and Rosendahl, 1359 (MIN); Bow River, Calgary, A. J. Breitung, 5075 (DAO); Red Deer River, J. Macoun, 1620 (DAO); North Saskatchewan River, Fort Saskatchewan, G. H. Turner, 2928 (DAO); Athabaska River, 3 miles north of Jasper, L. Jenkins, 5905 (DAO); Exshaw, W. C. McCalla, 11526 (ALTA); Roadside, Jasper Park, E. H. Moss, 4771 (ALTA); Jasper National Park, Scamman, 3365 (US); Bow River, Banff, W. C. McCalla, 2384 (US); Banff townsite, W. C. McCalla, 2385 (US); Yarrow Creek north of Waterton Park, E. H. Moss, 701 (US); 2 miles west of Fort Saskatchewan, G. H. Turner, 5423 (CAN); Bank Bow River, Calgary, W. C. McCalla, 4367a (CAN); South Kootenay Pass, Rocky Mountains, Dawson, August 9, 1881 (CAN); Bow River, Calgary, J. Macoun, June 5, 1897 (CAN); Caribou Mountains, Raup, 2178 (CAN); Crow's Nest Pass, Rocky Mountains, J. Macoun, August 17, 1897 (CAN); Banff, S. Brown, 130 (US); Lake Beauvert, Jasper Park, J. G. Jack, 2556 (US); Woods, Red Deer River, A. H. Brinkman, 2106 (US); Blakiston Brook, Waterton Park, E. H. Moss, 595 (US); Campsite near Crow's Nest Pass, Rocky Mountains, J.R.D. 2278, 2279 (ALTA);

Campsite 13 miles east of Canmore, J.R.D. 1354 (ALTA); Red Lodge Provincial Park, J.R.D. 1361, 1362 (ALTA); Marsh along Red Rock Canyon Road, Waterton National Park, J.R.D. 1645, 1646, 1647, 1648 (ALTA); Forestry Road southwest of Nordegg, J.R.D. 1333, 1334, 1335, 1337 (ALTA); Red Rock Canyon, Waterton National Park, J.R.D. 1649, 1650 (ALTA); Roadside, Red Rock Canyon Road, Waterton National Park, J.R.D. 1673, 1674, 1675, 1676 (ALTA); High River, J.R.D. 1680, 1681 (ALTA); Pyramid Lake, Jasper National Park, J.R.D. 1751 (ALTA); 23 miles north of Jasper, Jasper National Park, J.R.D. 1757, 1758, 1759 (ALTA); Rocky River Campground, Jasper National Park, J.R.D. 1760 (ALTA); North of Rocky River campground, Jasper National Park, J.R.D. 1761, 1762, 1763, 1764 (ALTA); Near north entrance to Jasper National Park, J.R.D. 1911, 1913 (ALTA); South of north entrance to Jasper National Park, J.R.D. 1917, 1918, 1919 (ALTA); Mile #7, Celestine Lake road, Jasper National Park, J.R.D., 1935, 1936, 1937, 1938, 1939 (ALTA); Vermilion Lakes, Banff National Park, J.R.D., 2026 (ALTA); Loop Road, Banff, Banff National Park, J.R.D. 2063, 2064, 2065, 2066 (ALTA); Pocahontas, J.R.D., 2320 (ALTA); Roadside, south of Pocahontas in Jasper National Park, J.R.D. 2242 (ALTA); Jasper House Historical marker, Jasper National Park, J.R.D. 2243, 2244, 2321 (ALTA); Pyramid Island, Pyramid Lake, Jasper National Park, J.R.D. 2253 (ALTA); Bow River, Canmore, J.R.D., 2259, 2260 (ALTA);

Lundbreck Falls, J.R.D. 2274, 2275, 2276, 2277 (ALTA).

SASKATCHEWAN: Maple Creek, A. J. Breitung, 4263 (DAO); Frenchman River, Cypress Hills, A. J. Breitung, 5484 (DAO); Big Muddy Valley, 7 miles from Montana border, W. Shevkenek 127 (DAO); Sandhills at MacDowall, J. S. Rowe, 542 (DAO); South Saskatchewan River, south of Saskatoon, Ledingham, 916 (DAO); Island, Lake Athabaska, Harper, 54 (US); McFarlane River sandhills, Lake Athabaska, Harper, 104 (US); Near South Saskatchewan River, north of Sutherland, L. Jenkins, 1217 (DAO); 8 miles S.W. of Saskatoon, R. T. Coupland, 192 (DAO).

MANITOBA: Gillam, Churchill District, Schofield, 1510 (DAO); Sandhills near Aweme, J. Fletcher, June 20, 1903 (DAO); Gillam, along Kettle River, W. Krivda, G-119 (DAO); East of Eriksdale, A. and D. Löve, 5564 (US).

NORTHWEST TERRITORIES: Great Bear Lake: north shore of McTavish Arm, A. E. and R. T. Porsild, 5230 (CAN).

YUKON TERRITORY: Halfway Lakes area, 15 miles north of Mayo, Calder and Gillett, 4242 (DAO); Dawson, Eastwood, 433 (MIN); McQuesten Area, east of White Mountain, J. D. Campbell, 177 (CAN); Dawson, M. O. Malte, 277 (CAN); Canol Road, Rose-Lapie River Pass, A. E. Porsild and A. J. Breitung, 10.058 (CAN).

ALASKA: Healy Quadrangle, 17 miles east of Cantwell on the Denali Hwy., G. W. Argus, 705 (DAO); Nabesna road, mile 89, Dutilly, LePage, and O'Neill, 21517 (CAN);

Franklin, Fortymile district, J. P. Anderson and G. W. Gasser, 7338 (CAN).

OREGON: 20 miles south of Maupin, Wasco Co., E. I. Applegate, 8248 (DAO).

IDAHO: Lewiston, Nez Perces Co., A. A. and E. Gertrude Heller, 3062 (DAO); Bay Horse Creek, L. F. Henderson, 3618 (A); Bannock Co., Mink Creek Canyon, 5 miles south of Pocatello, R. L. Lingenfelter, 622 (DAO).

COLORADO: F. E. and E. S. Clements, 219 (DAO).

MONTANA: Lewis and Clark Co., 25 miles N.W. of Augusta, C. L. Hitchcock, 18045 (DAO); Yellow Bay, Flathead Lake, M. E. Jones, 9085 (A).

WYOMING: Albany Co., Sybille Creek in canyon in Laramie Range, C. L. Porter, 6857 (DAO).

UTAH: Hidden Lake, near Glendale, M. E. Jones, 25130 (A).

NORTH DAKOTA: Vim, Slope Co., Potter and Greene, August 4, 1958 (DAO).

BETULA GLANDULOSA Michaux, Fl. Bor. Amer. 2:180 (1803)

Hooker, Fl. Bor. Am. 2:156 (1839); Watson, Botany Vol. II Geol. Surv. of Calif. 80 (1880), in part; Rydberg, Flora of Montana and the Yellowstone National Park 116 (1900); Winkler in Engler, Pflanzenreich, IV. 61 (Heft 19):73 (1904), pl. sibir. exclud. (- B. gl. var. sibirica (Ledeb.) Schneid.); Butler, Bull. Torrey Bot. Club 36:424 (1909); Rydberg, Fl. of the Prairies and Plains of Central North Am. 260 (1932); Raup, Contrib. Arnold Arb. VI:152 (1934); Abrams, Illustrated Fl. of the Pacific States Vol. I: 511 (1940); Anderson, Fl. of Alaska 218 (1942); Hultén, Fl. of Alaska and Yukon 4: 573 (1944); Raup, Sargentia VI:163 (1947); Fernald, Gray's Manual of Botany 536 (1950) in part; Porsild, National Museum of Canada Bull. No. 121:151 (1951); National Museum of Canada Bull. No. 146:70 (1957); Davis, Fl. of Idaho 236 (1952); Gleason, The New Britton and Brown Illustrated Fl. of the Northeastern United States and Adjacent Canada Vol. 2:36 (1952); Harrington, Fl. of Colorado 180 (1954), in part; Breitung, Am. Midland Naturalist 58:25 (1957); Moss Fl. of Alberta 185 (1959); Krüssmann, Handbuch der Laubgehölze, 232 (1962).

B. nana var. intermedia Regel, Nouv. Mem. Soc. Nat. Moscou, 13,2:102, t. 9, fig. 6,8,16,17,19-26a (Monog. Betul. 44) (1861).

B. glandulifera Sharples, Alaska Wild Flowers 24 (1938).

B. glandulosa Michx. var. *glandulosa* Wiggins and Thomas, Fl. Alaskan Slope, 151 (1952).

Low shrub, 3-15 dm tall, erect or prostrate, matted; branchlets coarse, reddish brown to gray, densely covered with whitish resinous glands, glabrous but more frequently with scattered long white to black hairs. Bark not exfoliating, dark brown to brownish black, dull. Winter buds ovoid, acute, very resinous, chestnut-brown, 1-2 mm long. Leaves usually dark green on both surfaces, turning orange to dark purplish red in autumn, broadly ovate to orbicular, 5-20 mm long, 5-15 mm wide, rounded at apex, crenate, usually less than 10 crenations along each margin, usually rounded at the base, coriaceous, glutinous, glandular dotted beneath, slightly reticulate; stomata averaging from 19-31 μ; petioles reddish, 1-5 mm long; smooth and often resinous coated; stipules ovate acute, ciliate, becoming scarious. Staminate catkins solitary 4-7 mm long during the winter, with ovate, dark green glandular bracts, ciliate on the margins, the catkins becoming 10-20 mm long at anthesis; pollen averaging from 15-25 μ in diameter. Pistillate catkins short-stalked, less than 10 mm long in flower; in fruit, 10-15 mm long, 4-6 mm wide, erect, ovoid to narrow cylindrical, obtuse, bracts finely ciliate, puberulent, lobes divergent, rounded at the apices, lateral lobes nearly as long as the middle lobe; body of the samara ovate to orbicular, 1-1.5 mm long, 1-1.5 mm wide, twice as wide as the wing. Chromosome number 2n = 28.

Types: Holotype: Specimen not seen, location unknown.

Type locality: "_Hab_. _circa_ _lacus_, _a_ _sinu_ _Hudsonis_ _ad_ _Mistassinis_".

Distribution: Bogs and rocky barrens in mountains and northern areas; British Columbia, Alberta, Saskatchewan and Manitoba; north throughout the Northwest Territories, Yukon Territory and Alaska; south in mountain ranges to northeastern California and Colorado, and east to Maine, Newfoundland, and southern Greenland. See Figure 2.

Taxonomic _Notes_: _Betula_ _glandulosa_ hybridizes with: _B_. _pumila_ var. _glandulifera_ (_B_. x _sargentii_);see page 92, 159, _B_. _fontinalis_ (_B_. x _eastwoodae_); see page 97, 172.

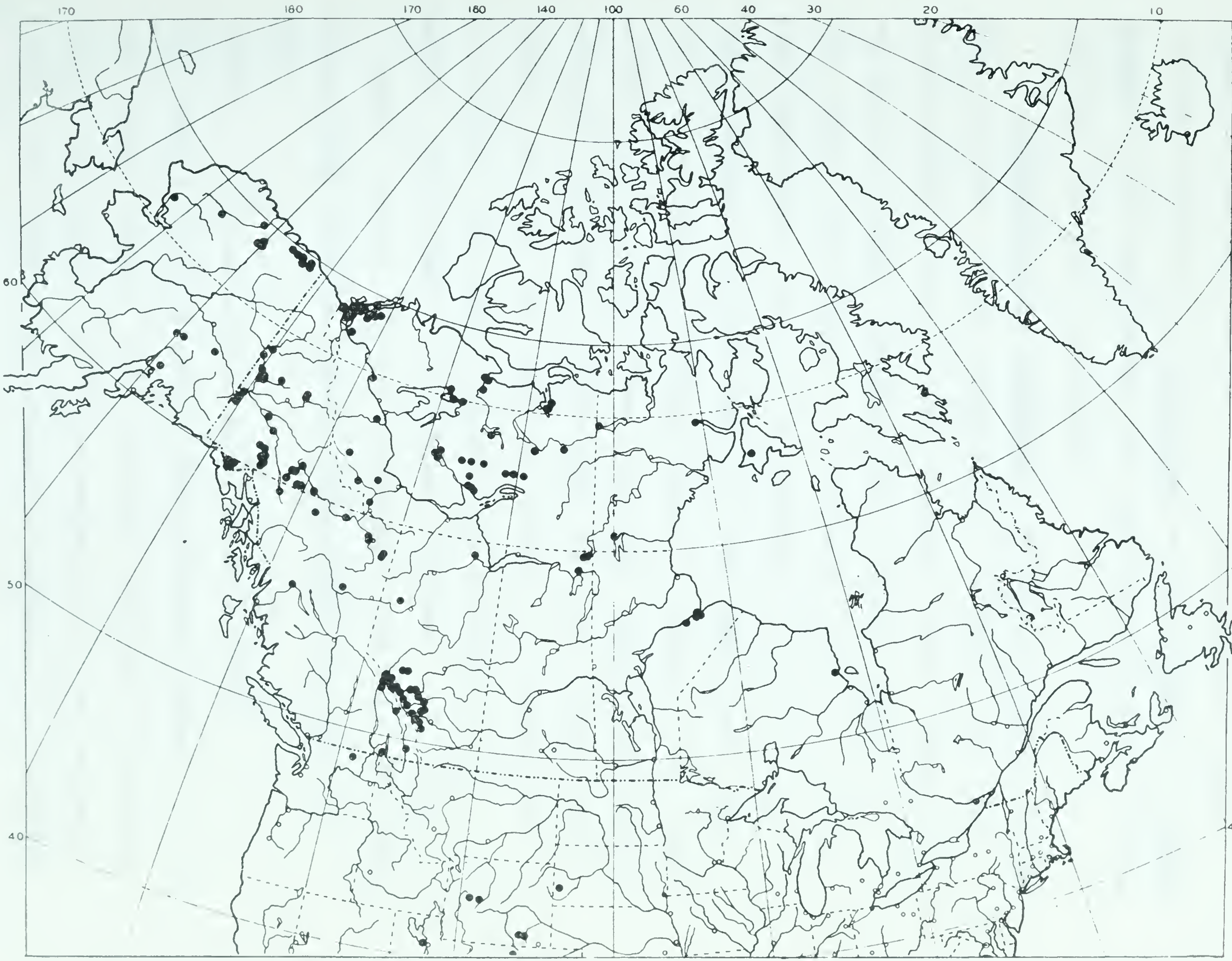
In addition Hultén (1944) has described _B_. _glandulosa_ x _B_. _nana_ var. _exilis_ and _B_. _glandulosa_ x _B_. _resinifera_. With regard to the latter, it would appear, following an examination of some of the specimens cited by Hultén, that they are more likely to be _B_. _fontinalis_ or _B_. x _eastwoodae_, although it is likely that such a hybrid does occur.

There is a close relationship between _Betula_ _glandulosa_ and _B_. _pumila_ var. _glandulifera_ (page 53). One of the characters which has been commonly used to distinguish _B_. _glandulosa_ from _B_. _pumila_ var. _glandulifera_ is the pubescence on the branchlets. This character is not consistent and a certain amount of pubescence consisting of mixed white to black hairs was found by the author in material of all her collections of these two species and their hybrids. Consequently use of this

FIGURE 2.

Distribution of Betula glandulosa.

(in N.W. North America)


170
180
170
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40

character has been avoided. The characteristics used in the descriptions of B. glandulosa and B. pumila var. glandulifera are the conclusions from detailed analytical studies described beginning on page 159 .

Representative specimens: BRITISH COLUMBIA: Haines Road, mile 60, Taylor, Szczawinski, and Bell, 1172 (DAO); Alaska Highway, Beaton River Crossing, Taylor, Szczawinski, and Bell, 45 (DAO); Burgess Pass, F. Fyles, August 31, 1914 (DAO); Fort Nelson, J. M. Gillett and D. A. Mitchell, 2968 (MIN) (DAO); Atlin, H. B. MacGregor, June 15, 1899 (DAO); Montney, H. Groh, Sept. 5, 1934 (DAO); Near Berg Lake, Mount Robson Provincial Park, L. Jenkins, 7162 (DAO); Alaska Highway, Summit Pass, Mile 392, Taylor, Szczawinski, and Bell, 100 (DAO); Haines Road, mile 75, Taylor, Szczawinski, and Bell, 809 (CAN); Mt. Selwyn, H. M. Raup and E. C. Abbe, 3759 (CAN); Sidley, west of Midway, J. M. Macoun, 79530 (CAN); Springhouse, Cariboo, J. A. Munro, 53 (CAN); Cassiar, Taylor, Szczawinski, and Bell, 364 (DAO); Haines Road, mile 98, Taylor, Szczawinski, and Bell, 961 (DAO).

ALBERTA: 19 miles west of Rocky Mountain House, J. R. D., 1330 (ALTA); 21 miles west of Rocky Mountain House, J. R. D., 1332 (ALTA); Cripple Creek campsite, southwest of Nordegg, J.R.D., 1344 (ALTA); Elk Creek campsite, S.W. of Nordegg, J.R.D., 1349 (ALTA); Near Waiparous campsite, S.W. of Nordegg, J.R.D., 1353 (ALTA); 23 miles S.W. of Edson on Coalbranch

Road, J. R. D., 1873, 1876, 1877, 1879, 1880, 1881, 1883 (ALTA); 38 miles southwest of Edson on Coalbranch Road, J. R. D., 1896, 1898, 1902, 1903 (ALTA); Campsite 21 miles north of Lower Waterfowl Lake, Jasper National Park, J. R.D., 1971, 1978, 1985 (ALTA); Bow Lake, Banff National Park, J. R. D., 2007, 2008, 2009, 2010 (ALTA); Pyramid Island, Pyramid Lake, Jasper National Park, J. R. D., 2252 (ALTA); Water Fowl Lake, Banff National Park, J. R. D., 2258 (ALTA); Mile 16, Kananaskis Road, J. R. D., 2262 (ALTA); Muskeg, Caribou Mountains, E. H. Moss, 9339 (DAO) (ALTA); S.W. of Ft. Smith, W. J. Cody, 3606 (ALTA); Sunwapta Pass, Jasper National Park, E. H. Moss, 4893 (ALTA) (DAO); Near Athabasca glacier, Jasper National Park, E. H. Moss, 4486 (DAO) (ALTA); Bow River Forest Reserve west of Turner Valley, J. J. Sexsmith, 222 (ALTA); Amongst rocks on river flat, Sunwapta River, Jasper National Park, E. H. Moss, 10955 (ALTA); Salt Plain, Bear Spring, Wood Buffalo Park, H. M. Raup, Aug. 19, 1930 (ALTA); Banff, F. J. Lewis, June, 1916 (ALTA); Between Water Valley and Cremona, north of Cochrane, W. C. McCalla, 10525 (ALTA); Stampeder Ranch, Highwood River Road, W. C. McCalla, 11966 (ALTA); Bow Valley, W. C. McCalla, 2383 (ALTA); Bow Valley, Banff National Park, W. C. McCalla, 9112, 9112A (ALTA); Subalpine brook, Laggan, H. C. Cowles, 142 (US); Ledum bog along highway 1 near Sunwapta Falls, Jasper National Park, Shirley Cotter, 3155 (MIN); Boggy meadow at Bow Summit, between Mistaya and Bow River Valleys, W. A.

Weber, 2466 (CAN); Jasper, M.O. Malte, July 28, 1917 (CAN); Laggan, M.O. Malte, 11.7.13 (CAN); White Mud Creek, North of Peace River, J. M. Macoun, 61,272 (CAN); Jumping Pound Creek, J. M. Macoun, 24,372 (CAN); Hand Hills, J. M. Macoun, 23,835 (CAN); Old man River, Dawson, 23838 (CAN); Mt. Edith, Banff, J. Fletcher, July 8, 1902 (DAO); Foot of Mt. Eisenhower, Banff National Park, A. and D. Löve, 6676 (DAO).

SASKATCHEWAN: East Oblate Lake, 59°49'N., 104°30'W., Scotter, 484 (DAO); S.E. Grove Lake, Scotter, 436 (DAO).

MANITOBA: Duck Lake, 59°22'N.,97°46'W., H. J. Scoggan and W.K.W. Baldwin, 8293 (ALTA); Baraizon Lake, H. J. Scoggan and W.K.W. Baldwin, 8195 (ALTA).

NORTHWEST TERRITORIES: Coppermine, W. I. Findlay, 47 (MIN) (ALTA); Southampton Island, Coral Harbor, W. J. Cody, 1218 (ALTA); Frobisher Bay, Baffin Island, H.A. Senn, 3664 (ALTA); Frobisher Bay, Ward Inlet, Hudson Bay Post, T.N. Freeman, July 19, 1948 (ALTA): Cobalt Island, Great Bear Lake, E. H. Moss, June 27, 1945 (ALTA); Artillery Lake, R. H. Bedford, July 11, 1924 (ALTA); Chesterfield, Eva Beckett, 343 (MIN); Pelly Lake, Eva Beckett, 531 (ALTA); Mackenzie River Delta: Kittigazuit Island, A.E. and R.T. Porsild, 2341 (CAN); Lake-on-the-Mountain, J.W. Thieret, R.J. Reich, 5845 (CAN); Vicinity of Brintnell Lake, H.M. Raup and J.H. Soper, 9341 (CAN); Bocks River, J. Carroll, 32 (CAN); Yellowknife Res., J. Carroll, 16 (CAN); Yellowknife Reserve, J. Carroll, 14 (CAN); Victoria Island: S.W. coast, vicinity of Holman

Island trading post, A.E. Porsild, 17274 (CAN); Great Bear Lake: north shore of McTavish Arm, A.E. and R.T. Porsild, 5231 (CAN) (US); Mackenzie River: north of Campbell Lake, A. E. and R.T. Porsild, 1907 (US); Bloody Falls on Coppermine River, W.I. Findlay, 138 (US); Mackenzie River Delta: N.E. shore of Richards Island, Kidluit Bay, W. J. Cody and D.H. Ferguson, 10153 (DAO); Toker Pt., 69°38'N., 132°54'W., W.J. Cody and D.H. Ferguson, 10295 (DAO); Eskimo Lakes: Portage Point, east side of westernmost lake, W.J.Cody and D.H. Ferguson, 10847 (DAO); Eskimo Lakes, 68°54'N.,133°14'W., W.J. Cody and D.H. Ferguson, 10606 (DAO); "Moose Lake", Eskimo Lake Basin, W. J. Cody, 10141 (DAO); Mackenzie River Delta: N.E. side of Richards Island, Kidluit Bay, W. J. Cody and D. H. Ferguson, 9964 (DAO); Tuktuk (Port Brabant), W. J. Cody and D. H. Ferguson, 9877 (DAO); Yellowknife, W. J. Cody, 2524 (DAO); Indin Lake, W. J. Cody and J.B. McCanse, 3452 (DAO); Muskox Lake, Back River, J. G. Chillcott, 172 (DAO); Caribou Hills, I. McT. Cowan, 13, July '47 (DAO); Coppermine, W. I. Findlay, 64 (DAO); Bathurst Inlet, W. I. Campbell, 70 (DAO); Yellowknife, W. J. Cody and J.B. McCanse, 2082 (DAO); Mile 74E Canol Road, Mackenzie Mts., Metro Tomasky, 2 (DAO); Vicinity Lake-on-the-Mountain, John W. Thieret, and R. J. Reich, 5811, 5845, 5868 (DAO); Yellowknife, W. J. Cody and J. B. McCanse, 2116 (DAO); Yellowknife, Baker Creek at Giant Mine, W. J. Cody and J. B. McCanse, 2146 (DAO).

YUKON TERRITORY: Whitehorse, Lewes River, A. E. Porsild and A. J. Breitung, 9.163 (CAN); Mountains north of McQuesten River, R. L Christie, 29 (CAN); McQuesten Area, S.E. of White Mt., creek flat, J. D. Campbell, 144 (CAN); Lake Kluane to Don Jek River, Adolf Müller, August 11-27, 1920 (US); Dawson, M. O. Malte, 90 (US).

ALASKA: Sadlerochit River, L.A. Spetzman, 1127a (MIN); 69°20'N., 145°00'W., L.A. Spetzman, 657 (MIN); North end of Wonder Lake, McKinley National Park, Ynes Mexia, 2234 (MIN); Flat north of Savage Camp, McKinley National Park, Ynes Mexia, 2108 (MIN); Lake Schrader, L.A. Spetzman, 686 (MIN); Ipnavik R., Irv. Tailleur, 10 (MIN); Umiat, Colville R., L. A. Spetzman, 2329 (MIN); Canning River canyon, L.A. Spetzman, 415 (MIN); Anaktuvuk Pass, L. A. Spetzman, Jul. 10, 1949 (MIN); Sadlerochit R., L. A. Spetzman, 1127b (MIN); Ignek Valley, L. A. Spetzman, 997 (MIN); Kanayut Lake, L. A. Spetzman, 1996 (MIN).

WYOMING: Near Little Brooklyn Lake, Medicine Bow Mts., Albany Co., Aven and Ruth Nelson, 2313 (DAO); Sublette Co., shore of Horseshoe Lake, western slope of Wind River Range southeast of Pinedale, C. L. Porter and B. F. Miller, 6098 (DAO); Fremont Co., Atlantic Creek, southern Wind River Mountains, C. L. Porter, 5605 (DAO); Bank of Nash Fork Creek near University of Wyoming Science Camp grounds, above Centennial, E. C. and T. G. Yuncker, 12012 (DAO).

COLORADO: Boulder Co., 8 miles N.W. of Nederland, W. A.

Weber, 5501 (DAO).

UTAH: American Fork Canon, Marcus E. Jones, July 16, 1895 (DAO).

SOUTH DAKOTA: Nahant, Aven Nelson, 590 (DAO).

<u>BETULA</u> <u>PUMILA</u> Linnaeus, Mant. 1: 124 (1767)

<u>B</u>. <u>PUMILA</u> var. <u>GLANDULIFERA</u> Regel, Bull. Soc. Nat. Moscou, 38,2: 410 (1865)

Winkler in Engler, Pflanzenreich, IV. 61 (Heft 19): 71 (1904); Abrams, Illustrated Flora of Pacific States, 511 (1940); Raup, Sargentia VI: 163 (1947); Fernald, Gray's Man. of Botany, 536 (1950); Davis, Flora of Idaho, 236 (1952); Breitung, Am. Midland Naturalist 58:25 (1957); Moss, Flora of Alberta, 185 (1959).

<u>B</u>. <u>glandulifera</u> (Reg.) Butler, Bull. Torrey Bot. Club 36: 424, fig. 2 (1909); Rydberg, Flora of the Prairies and Plains of Central North America 260 (1932); Krüssmann, Handbuch der Laubgehölze 231 (1962).

<u>B</u>. <u>obovata</u> Butler, Bull. Torrey Bot. Club 36:427, fig. 5 (1909).

<u>B</u>. <u>glandulosa</u> var. <u>glandulifera</u> (Regel) Gleason, The New Britton and Brown Illustrated Flora of Northeastern U. S. and Adjacent Canada Vol. 2: 36 (1952).

<u>B</u>. <u>glandulosa</u> Michx. <u>sensu</u> Watson, Botany Vol. II, Geol. Surv. of Calif. 80 (1880) in part; <u>sensu</u> Harrington, Flora of Colorado 180 (1954) in part.

<u>B</u>. <u>hallii</u> Howell, Fl. of N. W. Am. 1: 614 (1903); Butler, Bull. Torrey Bot. Club 36: 428, fig. 6 (1909); Krüssmann, Handbuch der Laubgehölze 232 (1962).

Shrub, 1-3 m tall, erect and spreading or somewhat prostrate and matted; branchlets slender, reddish brown, usually sparsely covered with yellowish resinous glands, puberulent or glabrous with some scattered long white to black hairs. Bark not exfoliating, dark brown, dull. Winter buds ovoid, acute, resinous, chestnut-brown, 2-3 mm long. Leaves dark green and shining above, pale to yellowish green below, turning rusty yellow in autumn, usually obovate, 2-4 cm long, 1-2 cm wide, usually cuneate at base, crenate to rarely serrate, with sinus between crenations rather broad, usually more than 14 crenations along each margin, more or less glandular dotted below, with peltate multicellular glands on both leaf surfaces, pubescent on the veins when young, finely reticulate; stomata averaging from 24-37 μ; petioles yellowish to reddish, 1-5 mm long, smooth, pubescent; stipules ovate, acute, ciliate, becoming scarious. Staminate catkins solitary, 5-10 mm long during the winter, with ovate to orbicular, dark brown puberulent bracts, ciliate on the margins, the catkin becoming 1.5-3 cm at anthesis; pollen averaging from 21-25 μ in diameter. Pistillate catkins short-stalked, about 12 mm long in flower; in fruit 2-3 cm long, 8-12 mm wide, erect, ovoid to cylindrical, obtuse, bracts finely ciliate, puberulent, lobes abruptly divergent, rounded lateral lobes shorter than the truncate middle lobe; body of samara ovate to obovate, 2-3 mm long, 1-2.5 mm wide,

scarcely wider than the wing. Chromosome number 2n = 56.

<u>Types</u>: Type specimen: Not seen, location unknown.

Type locality: North America.

<u>Distribution</u>: In bogs, especially sphagnum bogs; British Columbia, Alberta, Saskatchewan, Manitoba and western Ontario (and western Quebec in Fernald, 1950); into southern Northwest Territories, southern Yukon, and westward to Alaska; south in bogs to Washington, Oregon and east to Idaho, Wyoming, North Dakota, Minnesota, Wisconsin, Michigan and to northern New York. See Figure 3.

<u>Taxonomic Notes</u>: <u>Betula pumila</u> var. <u>glandulifera</u> hybridizes with:

<u>B</u>. <u>glandulosa</u> (<u>B</u>. x <u>sargentii</u>); see page 92, 159;

<u>B</u>. <u>resinifera</u> (<u>B</u>. x <u>uliginosa</u>); see page 89, 130; and

<u>B</u>. <u>papyrifera</u> (<u>B</u>. x <u>sandbergii</u>); see page 113, 220.

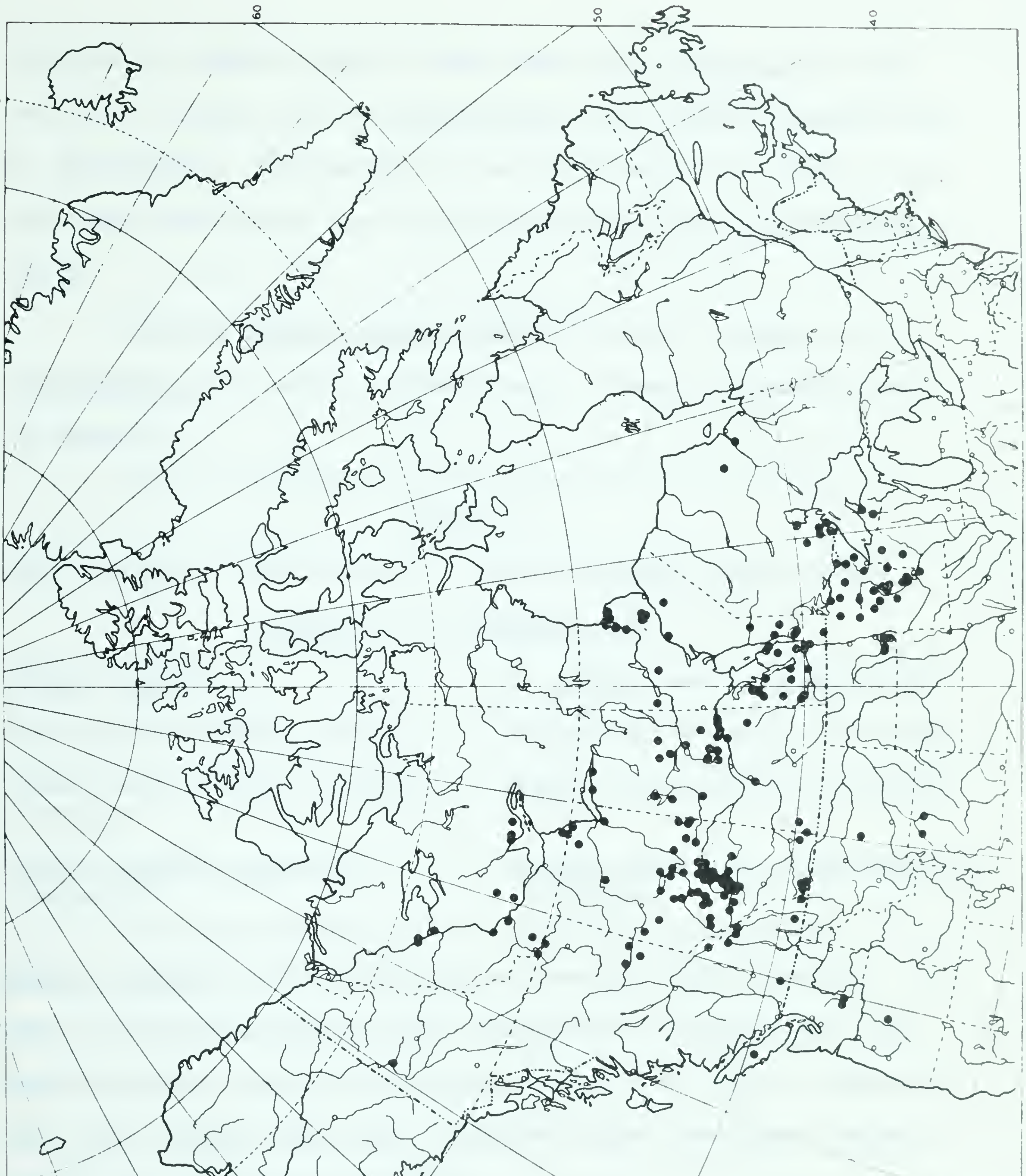
The latter hybrid was first described by Britton (1904) as a species, <u>Betula Sandbergii</u>, but its hybrid nature was demonstrated by Rosendahl in 1916 and 1928. This taxon has been the subject of a recent investigation by Clausen (1959, 1962, 1963).

It was outside of the range of the present study to consider the validity of the varietal status of var. <u>glandulifera</u>. It is possible that this birch should be a separate species, <u>B</u>. <u>glandulifera</u>, as it was considered by Butler (1909), or as a subspecies, but the old name is retained for convenience. Butler felt that it was more closely

FIGURE 3

Distribution of *Betula pumila* var. *glandulifera*.

(in N.W. North America)



related to several other forms than to B. pumila and this perhaps is true. It is apparently very closely related to B. glandulosa, from which it has been separated above, and has been considered as a variety of this species (Gleason, 1952).

Typical Betula pumila differs from B. pumila var. glandulifera in several characters. These are summarized in Table 2.

TABLE 2.

Morphological characters of typical Betula pumila and B. pumila var. glandulifera.

Betula pumila	B. pumila var. glandulifera
Branchlets without glands	Branchlets glandular resinous
Lower leaf surface without glands	Lower leaf surface glandular
Leaves mostly pubescent beneath	Leaves sparingly pubescent or glabrous

Betula pumila is found mostly in eastern North America, in bogs or wooded swamps, often calcareous; Ontario east to Newfoundland; south to northern Maine; and west to Connecticut, New Jersey, New York, northern Ohio, northern Indiana and Wisconsin (Fernald, 1950).

From the study of type specimens and the original descriptions, it has been determined that two previously described species, Betula obovata Butler (Plate a3) and B. hallii Howell (Plate a4) cannot be distinguished from B.

pumila var. _glandulifera_ and these names are synonyms.

Representative specimens: BRITISH COLUMBIA: Liard Hotsprings, A. E. and R. T. Porsild, 22029 (CAN); Hazelton, Skeena River, J. M. Macoun, July 18, 1917 (CAN); Muskeg along Carbon R., about 4 miles above the Peace, H. M. Raup and E. C. Abbe, 4261 (CAN); Between Flying U Ranch and Watch Lake, J. W. Eastham, 11.577 (CAN); Donald, Columbia Valley, J. M. Macoun, 23622, spec. a (CAN); Valley of Kicking Horse River, west of Field, W. C. McCalla, 9231 (ALTA); Sandy flats of Kicking Horse River, west of Field, W. C. McCalla, 9230 (ALTA).

ALBERTA: Bog near Leslieville, J. R. D., 1318, 1319, 1320, 1321, 1325 (ALTA); 6 miles west of Rocky Mountain House, J. R. D., 1328 (ALTA); Bog on Highway 43, 1 mile from Sangudo, J. R. D., 1405, 1408 (ALTA); Bog about 40 miles east of Slave Lake, J. R. D., 1453, 1454, 1455, 1456, 1457, 1458 (ALTA); Bog near Fedora, J. R. D., 1487, 1488, 1489, 1491, 1492, 1494 (ALTA); Bog 31 miles north of Highway 28, J. R. D., 1545, 1544, 1546, 1547 (ALTA); Bog between Turner and Cold Lake, J. R. D., 1558, 1559 (ALTA); Primrose Highway Bog, J. R. D., 1563, 1564, 1565, 1566, 1567, 1568, 1569 (ALTA); Bog near Gunn, J. R. D., 1606, 1607 (ALTA); Ponoka bog, J. R. D., 1682, 1683, 1684, 1687, 1688, 1692, 1693, 1708, 1711, 1713, 1714, 2157, 2170, 2177, 2180, 2183, 2189, 2190, 2191, 2192, 2173, 2205, 2208, 2210, 2216, 2219, 2304, 2307a, 2307, 2310, 2214, 2220, 2311, 2316, 2317, 2318 (ALTA); Campsite

west of Wildwood, J. R. D. 1715 (ALTA); 2½ miles south of Clymont school, west of Winterburn, J. R. D., 1776, 1779, 1780, 1781, 1782 (ALTA); 18 miles west of Wildwood campsite, J. R. D., 1867, 1869 (ALTA); 5 miles east of Edson, J. R. D., 1870 (ALTA); Bog near north entrance, Elk Island National Park, J. R. D., 2092, 2093, 2094, 2096, 2098, 2099, 2100, 2102, 2103 (ALTA); Bog, Elk Island National Park, J. R. D., 2115, 2117 (ALTA); White Mud Park, Edmonton, J. R. D., 2148, 2149 (ALTA); 8 miles north of Whitecourt, campsite, J. R. D., 2221 (ALTA); 2 miles northeast of Fort Saskatchewan, Turner, 5754, 5417, 7664 (ALTA); White Mud Creek Edmonton, E. H. Moss, 5089 (ALTA); Northwest of Spruce Grove, E. H. Moss, 11076 (ALTA); Cypress Hills, Twin Lakes, A. J. Breitung, 5268 (DAO); McLennan, H. Groh, Sept. 14, 1934 (DAO); Dem-mitt, W. D. Albright, 5 (DAO); 5 miles north of Fort Sas-katchewan, G. H. Turner, 22 (DAO); Fort Saskatchewan, G. H. Turner, 5433, 5571 (DAO); 2 miles N.E. of Fort Saskatche-wan, G. H. Turner 5441 (DAO); 15 miles north of Fort Saskatche-wan, G. H. Turner 5690 (DAO); 8½ miles N.E. of Fort Saskatche-wan, G. H. Turner, 5626 (DAO); Cypress Hills, south of Elkwater Lake, A. J. Breitung, 5632 (DAO); Ma-Me-O Beach on Pigeon Lake, G. H. Turner, 5870 (DAO); Beaverlodge, L. Jenkins, 435 (DAO); 2 miles S.W. of Ft. Smith, W. J. Cody and C. C. Loan, 4018 (DAO); Near Peace Point, Francis Harper, 129 (US); Waterton Lakes Park, swampy area, E. H. Moss, 655 (US); Spruce bog, Rocky River campsite, 21 miles

north of Jasper, F. J. Hermann, 13546 (US); Lake Louise Station, F. J. Hermann, 12699 (US); 2 miles S.W. of Ft. Smith, W. J. Cody and C. C. Loan, 4018 (US).

SASKATCHEWAN: 20 miles north of Montreal Lake, Melfort District, R. C. Russell, S 523 01 (DAO); Crossing of the Waterhen River, 25 miles north of Meadow Lake, A. J. Breitung, 8302 (DAO); Canora, E. W. Hart, 150 (DAO); Paddockwood, J. P. O'Hea, 1330 (DAO); Stony shore, Poplar Pt., Lake Athabaska, Francis Harper, 89 (US); Athabaska Lake, H. M. Laing, 241 (US); South shore of Lake Athabaska, west of McFarlane River, G. W. Argus, 761-62 (SASK).

MANITOBA: Eriksdale, 80 miles N.W. of Winnipeg, H. J. Scoggan, 9199 (ALTA); Nelson River, 20 miles N.E. of Norway House, H. J. Scoggan, 3101 (ALTA); Oxford Lake, 130 miles N.E. of Lake Winnipeg, H. J. Scoggan, 5307 (ALTA); Virden, H. Groh, July 25, 1921 (DAO); Bird's Hill, W. N. Denike, 103 (DAO); Cypress River, H. H. Marshall, 3 (DAO); North Winnipeg, W. N. Denike, C-3 (DAO); Arborg, A. Löve, 5319 (DAO); Gillam, W. B. Schofield, 1380, 1303 (DAO); Fort Churchill, J. C. Ritchie, 2161 (DAO); Mile 7, Norgate Road, Riding Mountain National Park, C. G. Riley, 50/606 (DAO); 4 miles east of Vannes, A. and D. Löve, 5569 (US).

ONTARIO: Highway 17, 4 miles east of English River, Pyramid Township, Thunder Bay District, Garton, 4420 (DAO); Rice Bay, Lac La Croix, Rainy River District, Garton, 5774 (DAO); Highway 120, 1 mile west of Nym Lake Road, Rainy River

District, Garton, 5041 (DAO).

NORTHWEST TERRITORIES: Enterprise-Mackenzie River Highway, Kakisa lake road, 3/4 mile from highway junction, J. W. Thieret, R. J. Reich, 4689 (DAO); West end of Cli Lake, W. J. Cody and K. W. Spicer, 12257 (DAO); Middle slope of Mount Flett, 32 miles north of Fort Liard, W. J. Cody and K. W. Spicer, 11900 (DAO); West shore of Liard River 14 miles S.W. of Fort Liard, W. J. Cody and K. W. Spicer, 11620 (DAO); West of Ft. Smith, W. J. Cody, 4176 (US) (ALTA) (DAO); Lagoon, Lower Hay River, W. H. Lewis, 738 (DAO) (ALTA); Norman Wells, W. J. Cody and R. L. Gutteridge, 7521 (DAO) (US) 7883 (DAO); Wood Buffalo Park, W. A. Fuller, 1955 (DAO); Fort Simpson Island, W. J. Cody and J. M. Matte, 9116 (DAO); Yellowknife, W. J. Cody, J. B. McCanse, 2549 (DAO); Enterprise-Mackenzie River Highway, mile 54, J. W. Thieret and R. J. Reich, 5075 (DAO); Enterprise-Mackenzie River Highway near Kakisa River, J. W. Thieret and R. J. Reich, 4770 (DAO); Enterprise-Mackenzie River Highway near mile 56, J. W. Thieret and R. J. Reich, 4797 (DAO); Mackenzie Lowlands: Liard River valley, 18 miles east of Liard River, W. W. Jeffrey, 249 (CAN); Great Bear River, south end of St. Charles Rapids portage, A. A. Lindsey, 559 (CAN).

WASHINGTON: South end of Black Lake, Thurston County, F. G. Meyer, 967 (DAO).

NORTH DAKOTA: Anselm, Ransom Co., O. A. Stevens, 1310 (DAO).

MINNESOTA: Ottertail County, J. W. Moore and B. O. Phinney, 12790 (DAO); South of Grand Lake, St. Louis Co., O. Lakela, 7963 (MIN); Basswood Lake, Lake Co., O. Lakela, 7986 (MIN); Ash River Road, Lake Kaketogama, St. Louis Co., O. Lakela, 10326 (MIN); St. Louis Co., O. Lakela, 11003 (MIN); Crooked Lake, St. Louis Co., O. Lakela, 12496 (MIN); 7 miles north of Underwood, Ottertail County, K. Clausen, 52 (MIN).

MICHIGAN: Malone Lake, Cheboygan Co., F. C. Gates, 21983 (DAO); Barago Co., Richards, 2959 (DAO); Road between Rice Lake and Grand Traverse Bay, Richards, 901 (DAO).

WISCONSIN: LaCrosse Co., Hartley, 2327 (DAO).

<u>BETULA</u> <u>RESINIFERA</u> Britton in Britton and Rydberg, Bull. N. Y. Bot. Garden 2: 165 (1901)

not <u>Betula</u> <u>alba</u> subsp. <u>verrucosa</u> var. <u>resinifera</u> Regel, Bull. Soc. Mosc. 18: 398 (1865); Anderson, Fl. of Alaska 219 (1942); Hultén, Fl. of Alaska and Yukon 4: 583 (1944).

<u>B</u>. <u>papyrifera</u> var. <u>humilis</u> (Regel) <u>sensu</u> Fernald and Raup, Rhodora 47: 321, t. 971, 972 (1945), not <u>Betula</u> <u>alba</u> subsp. <u>papyrifera</u> var. <u>humilis</u> Regel in DC Prodr. 16,2: 166 (1868); Raup, Sargentia VI: 162 (1947); Breitung, Am. Midland Naturalist 58: 25 (1957); Krüssmann, Handbuch der Laubgehölze, Band I: 235 (1962).

<u>B</u>. <u>pendula</u> var. <u>japonica</u>, <u>sensu</u> Fernald, Am. Jour. Sci. 8: 191 (1902).

<u>B</u>. <u>alaskana</u> Sargent, Bot. Gaz. 31: 236 (1901), Trees of N. Am. (1905) (reprinted Vol. 2: 217, 1962), not Lesquereux, U. S. Geol. Surv. of the Territories Vol. VIII: 258 (1883), fossil; Britton, N. Am. Trees, 249 (1908); Butler, Bull. Torr. Club 36: 434 Fig. 13 (1909); Sharples, Alaska Wild Fl. 24 (1938).

<u>B</u>. <u>neoalaskana</u> Sargent, Jour. Arnold Arb. 3: 206 (1922).

<u>B</u>. <u>papyrifera</u> var. <u>neoalaskana</u> (Sarg.) Raup, Contr. Arnold Arb. 6: 152 (1934); Porsild, National Museum of Canada Bull. No. 121: 154 (1951); Moss, Fl. of Alberta, 185 (1959).

Tree, usually 10-15 m, occasionally up to 30 m tall, trunk up to 4 dm in diameter, branches erect and spreading or pendulous; branchlets slender, glabrous, bright reddish brown and more or less thickly covered during the first year with resinous glands which are sometimes persistent during the second and third seasons. Bark thin, marked by numerous elongated dark, slightly raised lenticels, dull reddish brown to pinkish white on the outer surface, light red on the inner surface, varying from close to exfoliating into thin sheets. Winter-buds ovoid, obtuse at the gradually narrowed apex, light reddish-brown shining, often resinous glandular 2-3 mm long. Leaves trullate to deltoid-ovate, acuminate, base truncate, rounded or broadly cuneate, margin coarsely and often doubly glandular-serrate, dark green above, pale to yellow-green below, turning bright yellow in autumn, with peltate multicellular glands on the lower leaf surface, 3-8 cm long, 2-6 cm wide, with a slender midrib and primary veins pubescent or ultimately glabrous; stomata averaging from 20-29 μ; petioles often bright red, somewhat hairy at first, finally glabrous, about 25 mm long; stipules ovate, acute, ciliate, bright green, becoming scarious. Staminate catkins 1-3, clustered, sessile, 10-20 mm long in winter, becoming 20-50 mm long in the spring, bracts ovate, acuminate, puberulous, greenish to red with yellow margins; pollen averaging from 17-24 μ in diameter. Pistillate catkins in flower cylindrical,

slender, glandular, about 25 mm long on stout peduncles, in fruit glabrous, pendulous or spreading, 20-40 mm long, 8-12 mm wide; bracts ciliate, the lateral lobes wide-spreading, broad obovate and obtuse, middle lobe lanceolate acute to rounded. Fruit a samara, body 1-2 mm wide, 2-3 mm long, ovate, puberulent at the apex, much narrower than its wing. Chromosome number 2n = 28.

Types: Holotype: Dawson, R. S. Williams, Aug. 13, 1899 (NY, not seen by the author, may be mislaid).

Paratype: Ft. Selkirk, (Yukon Territory), J. B. Tarleton, No. 138, July 18, 1899 (US). (See Plate a5).

Distribution: Bogs, sandhills and sunny slopes, not in Rocky Mountains; northern British Columbia, Alberta, Saskatchewan and Manitoba; northward in Northwest Territories, Yukon and Alaska to tree line; southern margin in southern Alberta, Saskatchewan and Manitoba. See Figure 3.

Taxonomic Notes: *Betula resinifera* hybridizes with: *B. pumila* var. *glandulifera* (*B.* x *uliginosa*); see page 89, 130, *B. papyrifera* (*B.* x *winteri*); see page 109, 209.

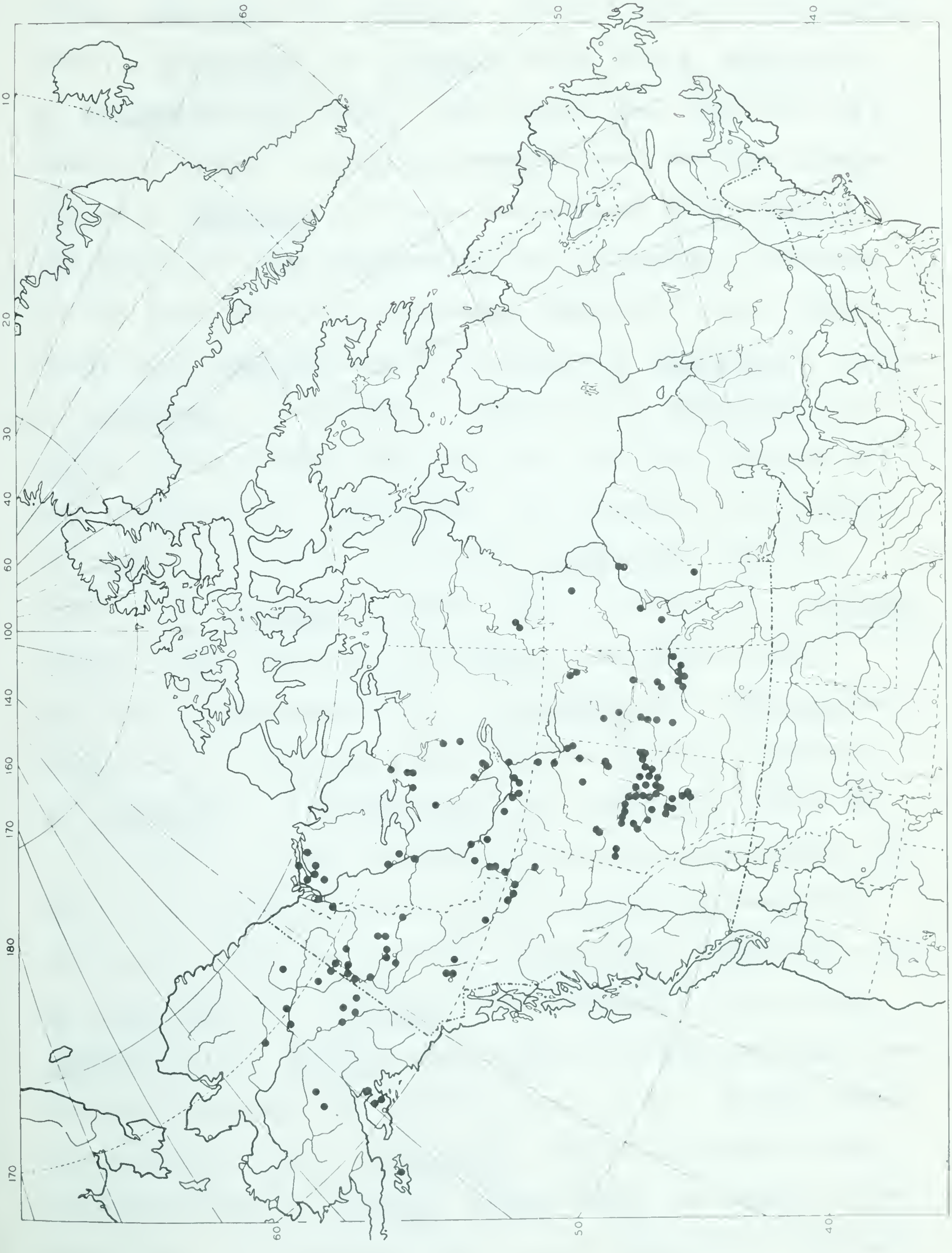
Hultén (1944) also listed hybrids with *B. kenaica* and *B. glandulosa* (see above).

It is possible that there is a relationship between the European *Betula verrucosa* (*B. pendula*) and *B. resinifera* as implied by Regel in describing *B. resinifera* as *B. alba*

FIGURE 4

Distribution of *Betula resinifera*.

(in N.W. North America)



60
50
40
10
20
30
40
60
100
140
160
170
180
170
60
50
40

subsp. *verrucosa* var. *humilis*. Fernald (1902), who listed both *B. resinifera* (*B. alaskana* Sarg.) and *B. kenaica* as *B. verrucosa*-type birches, has stated that these taxa are identical based on original descriptions, the type specimen of *B. alaskana*, and later collections of *B. kenaica* for which the type specimen was not available to Fernald. It has been found in the present study that later collections of *B. kenaica* seem to be partly *B. resinifera*, partly *B. papyrifera* (or perhaps a variety of *B. papyrifera*) and partly several hybrid entities, but the type specimen was not available for comparisons. The original descriptions of these two birches, those of *B. resinifera* (Britton, 1901) or *B. alaskana* (Sargent, 1901) and that of *B. kenaica* (Evans, 1899) are not very similar. Woodworth (1930) counted the chromosomes of *B. papyrifera* var. *kenaica* and found n = 35, the same number that he found for typical *B. papyrifera*. *B. resinifera* has a chromosome number of n = 14 which may be a distinguishing character between the two if we assume that the material counted by Woodworth (for which there are no herbarium specimens available) was *B. papyrifera* var. *kenaica*. The chromosome number of *B. papyrifera* var. *kenaica* (determined from seed obtained from Kew gardens under this label) is 2n = c 65. Hultén (1944) has reported that *B. resinifera*, common in inland Alaska, hybridizes with *B. kenaica*, common along the Alaskan coast. Apparently this hybridization is very extensive, and where

the two species are in contact Hultén feels that the hybrids are the most common birches encountered.

Representative specimens: BRITISH COLUMBIA: Liard Hotsprings, A. W. and R. T. Porsild, 22030 (CAN); Mile 496 Alaska Highway, A. E. Porsild, 9068 (CAN); Mile 497, Alaska Highway, Taylor, Szczawinski, and Bell, 328 (CAN). ALBERTA: 12 miles north of Ft. Fitzgerald, W. J. Cody and C. C. Loan, 4554 (ALTA) (DAO); Lac la Biche Mission, W. J. Cody and R. L. Gutteridge, 7039 (DAO), 7036 (ALTA); Dry muskeg south of Lac la Biche, W. J. Cody and R. L. Gutteridge, 6979 (DAO); 12 miles north of Ft. Fitzgerald, W. J. Cody and C. C. Loan, 4555 (DAO) (MIN); Gov. Hay Camp district, Slave River, H. M. Raup, 2181 (CAN); Base of eastern slope of Caribou Mountains, H. M. Raup, 2183 (CAN); Lake Vermilion, Peace River, F. L. Lawrence, 1907 (DAO); 20 miles east of Fort Saskatchewan, G. H. Turner, 7095 (DAO); 8½ miles N.E. of Fort Saskatchewan, G. H. Turner, 5607, 5612, 5608 (DAO); 15 miles north of Fort Saskatchewan, G. H. Turner, 5675, 5687, 5686, 5688, 5689 (DAO); 14 miles north of Fort Saskatchewan, G. H. Turner, 4967 (DAO); Fort Saskatchewan, G. H. Turner, 7084, 7083, 7082, 4832, 2485, 2379, 4771, 2359 (DAO); 8 miles N.E. of Fort Saskatchewan, G. H. Turner, 5620 (ALTA) (DAO), 5619 (DAO) (CAN); 9 miles N.W. of Fort Saskatchewan, G. H. Turner, 1911 (DAO) (ALTA); Ma-me-O Beach, Pigeon Lake, G. H. Turner, 5003 (DAO); Beaver Lodge, L. Jenkins, 698 (DAO); Kenzie north of High Prairie, E. H.

Moss, 7752 (DAO), 7742 (ALTA); Astoten Lake, Elk Island National Park, B. O'Connor and R. D. Ursher, 17-51 (DAO); Smith, E. H. Moss, 7375 (DAO) (ALTA); Nestow, E. H. Moss, 7376 (DAO) (ALTA); Fort MacMurray, Athabasca, A. E. Preble, M. Cary, 104 (US); Sand Pt., north shore of Lake Athabaska, H. M. Raup and E. C. Abbe, 4583 (CAN); West of Pembina River, W. Spreadborough, June 15, 1898 (CAN); 22 miles N.W. of Athabasca, W. C. McCalla, 11318a, 11318 (ALTA); North edge of Elk Island Park, W. C. McCalla, 10331a (ALTA); 4 miles east and 4 miles north of Fort Saskatchewan, G. H. Turner, 5607 (ALTA); Jackfish Lake about 5 miles north of Blackfalds, W. C. McCalla, 11392 (ALTA); Lac la Biche, W. J. Cody and R. L. Gutteridge, 7113 (ALTA); Muskeg, G. H. Turner, 1669 (ALTA); North shore of Lake Athabaska, H. M. Raup, E. C. Abbe, 4463 (ALTA); Between Pigeon Lake and Gull Lake, woods, J. R. D., 1304, 1308 (ALTA); Woods near Gunn on Lake Ste. Anne, J. R. D., 1394 (ALTA); Bog on Highway 43, 1 mile from Sangudo, J. R. D., 1402, 1403, 1404, 1406, 1407 (ALTA); Pembina River Park in Sangudo, J. R. D., 1412, 1413, 1414, 1415 (ALTA); Woods about 6 miles north of Whitecourt, J. R. D., 1422, 1423 (ALTA); near Triangle, J. R. D., 1425, 1426, 1427 (ALTA); Junction of Highway 34A and 2, J. R. D., 1428, 1430 (ALTA); 31 miles east of Junction of Highway 34A and 2, J. R. D., 1433, 1434 (ALTA); Joussard near Lesser Slave Lake, J. R. D., 1435, 1436 (ALTA); Faust, J. R. D., 1438, 1440 (ALTA); Assinou River Campsite,

J. R. D., 1442, 1443 (ALTA); Slave Lake, J. R. D., 1446, 1447, 1448, 1450 (ALTA); Campsite near Slave Lake, J. R. D., 1451, 1452 (ALTA); Campsite near Chisholm, J. R. D., 1461, 1464, 1465 (ALTA); Flatbush campsite, J. R. D., 1466, 1467, 1468 (ALTA); Bog near Fedora, J. R. D., 1490, 1493 (ALTA); Roadside near Newbrook, J. R. D., 1498, 1499 (ALTA); Long Lake, J. R. D., 1500, 1501, 1502, 1506, 1507, 1508, 1509, 1510 (ALTA); Flat Lake, J. R. D., 1517, 1518, 1519, 1520 (ALTA); Near Donatville, J. R. D., 1521, 1522, 1523, 1524 (ALTA); 1 mile from Beaver Lake, J. R. D., 1528, 1529 (ALTA); Beaver Lake bog, J. R. D., 1530, 1531, 1532 (ALTA); Lac la Biche, J. R. D., 1533, 1534 (ALTA); 6 miles north of Highway 28, J. R. D., 1537, 1538, 1539 (ALTA); 12 miles north of Highway 28, J. R. D., 1540 (ALTA); 15 miles north of Highway 28, J. R. D., 1542, 1543 (ALTA); Near Turner, J. R. D., 1550 (ALTA); Road from Turner to Cold Lake, J. R. D., 1551, 1552, 1553 (ALTA); Cold Lake Beach, J. R. D., 1560, 1561, 1562 (ALTA); Along Primrose Highway, J. R. D., 1570 (ALTA); Cold Lake, J. R. D., 1571, 1572, 1573 (ALTA); Provincial Campsite, Cold Lake, J. R. D., 1575, 1576, 1577, 1578, 1579, 1580 (ALTA); Junction Highways 28 and 45, J. R. D., 1582, 1583 (ALTA); Bog near Muir Lake, J. R. D., 1592, 1593 (ALTA); Bog near Gunn, J. R. D., 1604 (ALTA); Wabamun Lake Provincial Park, J. R. D., 1608, 1609, 1610, 1611, 1612 (ALTA); Gainford campsite, J. R. D., 1613 (ALTA); Pembina Provincial Park, J. R. D., 1614, 1615,

1616, 1617, 1618, 1619 (ALTA); Ponoka bog, J. R. D., 1685, 1686, 1690, 1697, 1699, 1702, 1707, 1712, 2166, 2168, 2175, 2184, 2186, 2187, 2204, 2211, 2213, 2306, 2308, 2309, 2312 (ALTA); Campsite west of Wildwood, J. R. D., 1716, 1717, 1718, 1719 (ALTA); 8 miles south of Winterburn, J. R. D., 1769, 1770, 1771, 1772 (ALTA); 2½ miles south of Clymont School, west of Winterburn, J. R. D., 1774, 1775, 1777 (ALTA); Thunder Lake, A. W. L. Stewart, 1783 (ALTA); White Mud Creek Picnic Ground, J. R. D., 1798, 1808 (ALTA); Wildwood campsite, J. R. D., 1852 (ALTA); 4 miles west of Wildwood campsite, J. R. D., 1853, 1854, 1855 (ALTA); 18 miles west of Wildwood campsite, J. R. D., 1864, 1865, 1866 (ALTA); Near main intersection, Elk Island National Park, J. R. D., 2082 (ALTA); Bog near north entrance, Elk Island National Park, J. R. D., 2091 (ALTA); Bog, Elk Island National Park, J. R. D., 2114, 2116 (ALTA); White Mud Creek Park, Edmonton, J. R. D., 2125, 2127 (ALTA); Emily Murphy Park, Edmonton, J. R. D., 2154, 2155, 2156 (ALTA); Campsite, Highway 14 near Edmonton, J. R. D., 2181 (ALTA); Two Creek campsite north of Whitecourt, J. R. D., 2222, 2223 (ALTA); Gunn campsite, J. R. D., 2224 (ALTA); Wabamun Provincial Park, A. W. L. Stewart, 2182 (ALTA).

SASKATCHEWAN: 7 miles east of McKague, A. J. Breitung, 669 (MIN); Shore of Nut Point, Lac la Ronge, G. F. Ledingham, 49-302 (DAO); 2 miles north of Greenbush, east of Greenbush River, A. J. Breitung, 717 (DAO); Wakesiu Lake, R. C. Russell,

June 5, 1938 (DAO); 20 miles north of Meadow Lake, A. J. Breitung, 8480 (DAO); 1 mile west of Golburn, A. J. Breitung, 1246, 1247, 1248, 677, 534, 567, 568, 675 (DAO); 4 miles south of Tisdale, A. J. Breitung, 1601, 1602 (DAO); 3 miles south of Tisdale, A. J. Breitung, 1541 (DAO); 4 miles west, 2½ miles north of McKague, A. J. Breitung, 904, 1286 (DAO); Beauvel, 150 miles north of Meadow Lake, A. J. Breitung, 8364 (DAO); 20 miles south of Meadow Lake, A. J. Breitung, 8181 (DAO) (ALTA); 3 miles south of Crooked River, A. J. Breitung, 630 (DAO); Golburn, A. J. Breitung, 535 (DAO); Ile La Crosse, Churchill River, A. J. Breitung, 8381 (DAO); Waterhen River Crossing, 25 miles north of Meadow Lake, A. J. Breitung, 8280 (DAO); McKague, A. J. Breitung, May 20, 1934 (DAO); Nipawin, A. J. Breitung, 6084 (DAO); 10 miles north of Meadow Lake, J. S. Rowe, 539 (DAO); 5 miles south of Tisdale, A. J. Breitung, 52 (DAO); 7 miles south of McKague, A. J. Breitung, 550 (DAO); Tisdale, A. J. Breitung, July 8, 1939 (DAO); N. E. Grove Lake, G. W. Scotter, 437A (DAO); N. Higginson Lake, G. W. Scotter, 423 (DAO); Vincinity of Quillwort Lake, south of Hasbala Lake, G. W. Argus, 1064-62 (SASK); Sunny Brow, J. Laycock (DAO); Nipawin, A. J. Breitung, 6070 (DAO); 2 miles west of Ennuyeuse Creek, Lake Athabaska, H. M. Raup, 6947 (ALTA); Vicinity of Patterson Lake, G. W. Argus, 463-63 (SASK).

MANITOBA: Esker at Big Spruce River at junction with Seal

River, J. C. Ritchie, 1845 (DAO); Sasaginnigak Lake, 175 miles N.E. of Winnipeg, A. J. Breitung, 7600 (DAO); Wabowden, mile 137, Hudson Bay Ry., J. M. Gillett, 2765 (DAO); Gillam, mile 326, Hudson Bay Ry., J. M. Gillett, 2683 (US) (DAO); Gillam, W. B. Schofield, 1426 (DAO); Herb Lake, woods around village on Wekusko Lake, H. J. Scoggan, 6468 (ALTA). NORTHWEST TERRITORIES: Reindeer Station, W. J. Cody and D. H. Ferguson, 10393, 9686, 10441 (DAO); Mackenzie Lowlands: Liard River valley, east shore, 6 miles below Fort Liard, W. W. Jeffrey, 486 (CAN); Eskimo Lakes, 68°43'N., 132°59'W., W. J. Cody and D. H. Ferguson, 10821 (DAO); Lac du Mort, G. W. Scotter, 1149 (DAO); Unnamed lake, 62°55'N., 111°55'W., G. W. Scotter, 1060 (DAO); 16 miles upstream from Reindeer Station, W. J. Cody and D. H. Ferguson, 9638 (DAO); Fort Simpson, W. J. Cody and J. M. Matte, 8674, 8654, 8883, 8431, 8191, 7995 (DAO); 42 miles north of Fort Liard, W. J. Cody and K. W. Spicer, 11931 (DAO); 30 miles downstream from Ft. Simpson, W. J. Cody and J. M. Matte, 8167 (DAO); Yellowknife, W. J. Cody, 2529 (DAO); Snare River Power Station, W. J. Cody, 2610 (DAO); Beaverlodge Lake, W. J. Cody, 2737 (DAO); Port Radium, Eldorado Mine, W. J. Cody, 2793 (DAO); Great Slave Lake, Hardisty Island, W. J. Cody and J. B. McCanse, 2921 (DAO); Outlet of Prosperous Lake, W. J. Cody and J. B. McCanse, 2876 (US) (DAO), 2887 (DAO); Great Bear Lake, Gunbarrel Inlet, W. J. Cody, 2825 (DAO); Yellowknife,

W. J. Cody and J. B. McCanse, 2365, 2055 (DAO); Yellowknife, west side of Kam Lake, W. J. Cody and J. B. McCanse, 2304 (DAO); Yellowknife, Joliffe Island, W. J. Cody and J. B. McCanse, 2304 (DAO); Yellowknife, Joliffe Island, W. J. Cody and J. B. McCanse, 2468 (DAO); Norman Wells, W. J. Cody and R. L. Gutteridge, 7402, 7840 (DAO); Lagoon, Lower Hay River, W. H. Lewis, 951, 950 (DAO); 5 miles upstream from Norman Wells, W. J. Cody and R. L. Gutteridge, 7590 (DAO) (ALTA); 2 miles upstream from Norman Wells, W. J. Cody and R. L. Gutteridge, 7562 (DAO); Norman Wells, near Bosworth Creek, W. J. Cody and R. L. Gutteridge, 7572 (DAO); Brabant Island, Great Slave Lake, W. H. Lewis, 1077, 1082 (DAO); Long Island, Great Slave Lake, W. H. Lewis, 789, 839 (DAO); Semenow Hills, W. H. Osgood, July 20, 1899 (US); Great Bear Lake, North shore of McTavish Arm, A. E. and R. T. Porsild, 5228 (US) (CAN); Fort Simpson, H. M. Raup and J. H. Soper, 9854 (CAN); 10 miles above Fort Liard in burned area, W. W. Jeffrey, 130 (CAN); Eskimo Lake Basin, S.E. of Setidgi Lake, A. E. and R. T. Porsild, 3142 (CAN); Mackenzie River Delta, E. Taylor, July, 1915 (CAN); N.W. extremity of Nueltin Lake, F. Harper, 2418 (CAN); Bank of Yellowknife Bay, A. L. Morrison, 52 (ALTA).

YUKON TERRITORY: Dawson, M. O. Malte, 93, 15 (CAN); Canol Road, mile 132, Lower Lapie River crossing, A. E. Porsild and A. J. Breitung, 9.539 (CAN); Near Dawson

City, R. G. McConnell, Aug., 1898 (CAN); Johnson's Crossing, M. P. Porsild, 778 (CAN); Dawson, A. Eastwood, 539a-59 (US) (CAN), 90, 498 (MIN); Ft. Selkirk westward to Dorijek River, M. W. Gorman, 976 (CAN); Bonanza Creek, Macoun, July 18, 1902 (CAN); McQuesten Area, McQuesten R., J. D. Campbell, 537 (CAN); Canol Road, Rose-Lapie R. Pass, mile 105, A. E. Porsild and A. J. Breitung, 9.245 (CAN); Haggart Creek, 22 miles NNW of Mayo, J. A. Calder, 2867 (DAO); Dawson, J.A. Calder and L. G. Billard, 2882 (US) (DAO), 2978 (DAO); Porter Creek, 3 miles north of Whitehorse, J. M. Gillett, 3481 (DAO); Whitehorse, J. M. Gillett, D.A. Mitchell, 3039 (DAO); About 3 miles north of Mayo, J. A. Calder, 4295 (DAO); Watson Lake, D. A. Mitchell, 107 (DAO); Bear Creek east of Dawson, J. Terasmae, June 25, 1961 (DAO); Dawson, A. Eastwood, 331-90, 272-89, 89, 90, 498 (US); Bonanza Creek bottom, J. Macoun, July 18, 1902 (US); Trail Eagle to Valdez, A. J. Collier, 76 (US); Fort Selkirk, M. W. Gorman, 976 (US); Canol Road, mile 132, Lower Lapie River Crossing, A. E. Porsild and A. J. Breitung, 9.540, 9.539 (US); Canol Road, Rose-Lapie River Pass, mile 105 near Lapie Lake, A. E. Porsild and A. J. Breitung, 9.245 (US); Canol Road, mile 222, Ross River valley near north end of Sheldon Lake, A. E. Porsild and A. J. Breitung, 11548 (US); Dawson, M. O. Malte, 92, 93 (A).

ALASKA: College, Olav Gjaerevoll, 904 (CAN); Roadside, Fairbanks, E. LePage, 23260 (CAN); Roadside, Slana-Tok

road, between Mantasta and Tok, Dutilly, LePage and O'Neill, 20474 (CAN); Adjacent to Alaska Highway, 52 miles east of Tanacross, H. J. Lutz, 1157 (CAN); Takotna, J. P. Anderson and G. W. Gasser, 7284 (CAN); Ft. Richardson, L. Spetzman, June 15, 1948 (MIN); Trail, Fairbanks to College of Agri-culture, Ynes Mexia, 2291 (MIN); Near center of north boundary of McKinley National Park, Ynes Mexia, 2262 (MIN); Anchorage, L. Spetzman, June 15, 1948 (MIN); Franklin, Forty-mile district, J.P. Anderson and G. W. Gasser, 7307, 7284 (DAO); 2 miles south of Circle, Dutilly, LePage, and O'Neill, 20925 (DAO); Lower ramparts of the Yukon, J. C. Russell, July 28, 1899 (US).

<u>BETULA</u> <u>PAPYRIFERA</u> Marshall, Arbust. Am. 19 (1785) Michaux, Flor. Bor. Amer. 2: 180 (1803); Regel in DeCandolle, 16: 165-166 (1868); Sargent, Silva N. Am. 9:57, t. 451 (1896); Rydberg, Fl. of Mont. and Yellowstone Natl. Park, 116 (1900); Britton, N. Am. Trees, 250 (1908); Butler, Bull. Torr. Bot. Club 36: 435 (1909); Raup, Cont. Arn. Arb. 6: 1-230 (1934); Fernald, Gray's Man. of Bot. 535 (1950); Gleason, New Brit. and Brown Illus. Fl. of N. E. U. S. and Adjacent Canada 2: 34 (1952); Moss, Fl. of Alberta, 185 (1959).

<u>B</u>. <u>papyracea</u> Aiton, Hort. Kew. 3: 337 (1789); Loudon, Arb. Brit. 3: 1708, fig. 1561 (1838); Nuttall, N. Am. Sylva Vol 1: 22-25 (1842); Dippel, Handb. Laubh. 177 (1892).

<u>B</u>. <u>excelsa</u> <u>sensu</u> Willdenow, Berlin. Baumz. 41, t.2, fig. 1 (1796); Sp. Pl. 4, 1: 463 (1805); not Aiton (1789).

<u>B</u>. <u>grandis</u> Schrader, Ind. Sem. Hort. Bot. Goetting. 1833: 2 (1833).

<u>B</u>. <u>latifolia</u> Tausch in Flora, 1838: 751 (1838).

<u>B</u>. <u>occidentalis</u> Hooker, Fl. Bor.-Am. 4: 155 (1838) in part; Lyall, Jour. Proc. Linn. Soc. 7: 134 (1864); Regel, Bull. Soc. Imp. Natur. 38: 400 (1865); Regel in De-Candolle Prodr. 16: 165 (1868); Howell, Fl. of N. W. Am., Vol. 1: 613 (1903) in part; Butler, Bull. Torr. Bot. Club 36: 437 (1909).

B. alba var. *papyrifera* (Marsh.) Spach in Ann. Sci. Nat. Bot. ser. 2, 15: 188 (1841).

B. papyrifera var. *lyalliana* Koehne *apud* Schelle, in Beissner, Schelle, and Zabel, Hand. Laubholz. Ben 55 (1903).

B. papyrifera var. *occidentalis* (Hooker) Sargent, Jour. Arn. Arb. 1: 63-65 (1919); Raup, Cont. Arnold Arb. 6:1-230 (1934).

B. papyracea var. *occidentalis* Dippel, Handb. Laubh. ii. 177 (1892).

B. alba subsp. *papyrifera* var. *communis* Regel in Bull. Soc. Nat. Moscou, 38,2: 401 (1865).

B. papyrifera var. a. *communis* (Reg.) f. *typica* Schneider, Ill. Handb. Laubh. 1: 115 (1904).

B. papyrifera var. a. *communis* f. *grandis* (Schrader) Schneider, Ill. Handb. Laubh. 1: 115 (1904).

B. papyrifera var. *commutata* (Regel) Fernald, in Rhod. 47: 312 (1945); Gray's Man. of Bot. 535 (1950); Raup, Sargentia 6: 162 (1947); Moss, Fl. of Alberta 185 (1959).

Tree, usually 20-30 m, occasionally up to 40 m tall, trunk up to 1 m in diameter, branches erect, spreading and pendulous; branchlets slender, viscid, greenish and covered with long pale hairs when they first appear, becoming dark orange to brown, glabrous or pubescent during the first year, gradually becoming darker and more glabrous in subsequent

years. Bark up to 1 cm thick at base of old trees, dark, furrowed; separating into thin scales, and higher on the tree creamy white, separating into thin sheets; orange inner layers. Winter buds ovate, acute, dark chestnut-brown, glabrous and slightly resinous, 2-3 mm long. Leaves ovate, acute to abruptly acuminate, base truncate, rounded or cuneate, margin coarsely and mostly irregularly doubly-serrate, dull green above, with multicellular peltate glands on the lower leaf surface, light green below, often with black glands, turning a light, clear yellow in autumn, 5-9 cm long, 4-6 cm wide, with a slender midrib and primary veins pubescent, with long white hairs when leaves unfold and finally with tufts of pale hairs in axils of veins; stomata averaging from 28-52 μ; petioles stout, yellow, somewhat pubescent, often with black glands, about 25 mm long; stipules ovate, acute, ciliate, light green, caducous. Staminate catkins 1-3 clustered, sessile, 20-30 mm long in winter, becoming 60-80 mm long in the spring, bracts ovate, acute to apiculate, puberulous, light brown to dark red-brown; pollen averaging from 24-26 μ in diameter. Pistillate catkins in flower cylindrical, slender, glandular, about 25 mm long on slender peduncles, in fruit glabrous, pendulous, 30-40 mm long, 8-12 mm wide; bracts glabrous, rarely puberulous, the lateral lobes wide-spreading, rounded, middle lobe lanceolate acute to rounded. Fruit a samara, body 1-2 mm wide, 2-4 mm long, ovate much

narrower than its wing. Chromosome number 2n = 56 - 84.

Types: Holotype: Not seen, its location unknown.

Type locality: Pennsylvania

Distribution: Forested areas; British Columbia, Alberta, Saskatchewan, Manitoba and eastward to Labrador; north to the tree line in Northwest Territories, Yukon and Alaska; south to Washington, Montana, Colorado, northern Nebraska, Minnesota, Wisconsin, Michigan, and northern Pennsylvania to New York. See Figure 4.

Taxonomic Notes: *Betula papyrifera* hybridizes with:
B. fontinalis (*B.* x *utahensis*); see page 101, 185,
B. x *sargentii* (*B.* x *arbuscula*); see page 107, 200,
B. resinifera (*B.* x *winteri*); see page 109, 209, and
B. pumila var. *glandulifera* (*B.* x *sandbergii*); see page 113, 220.

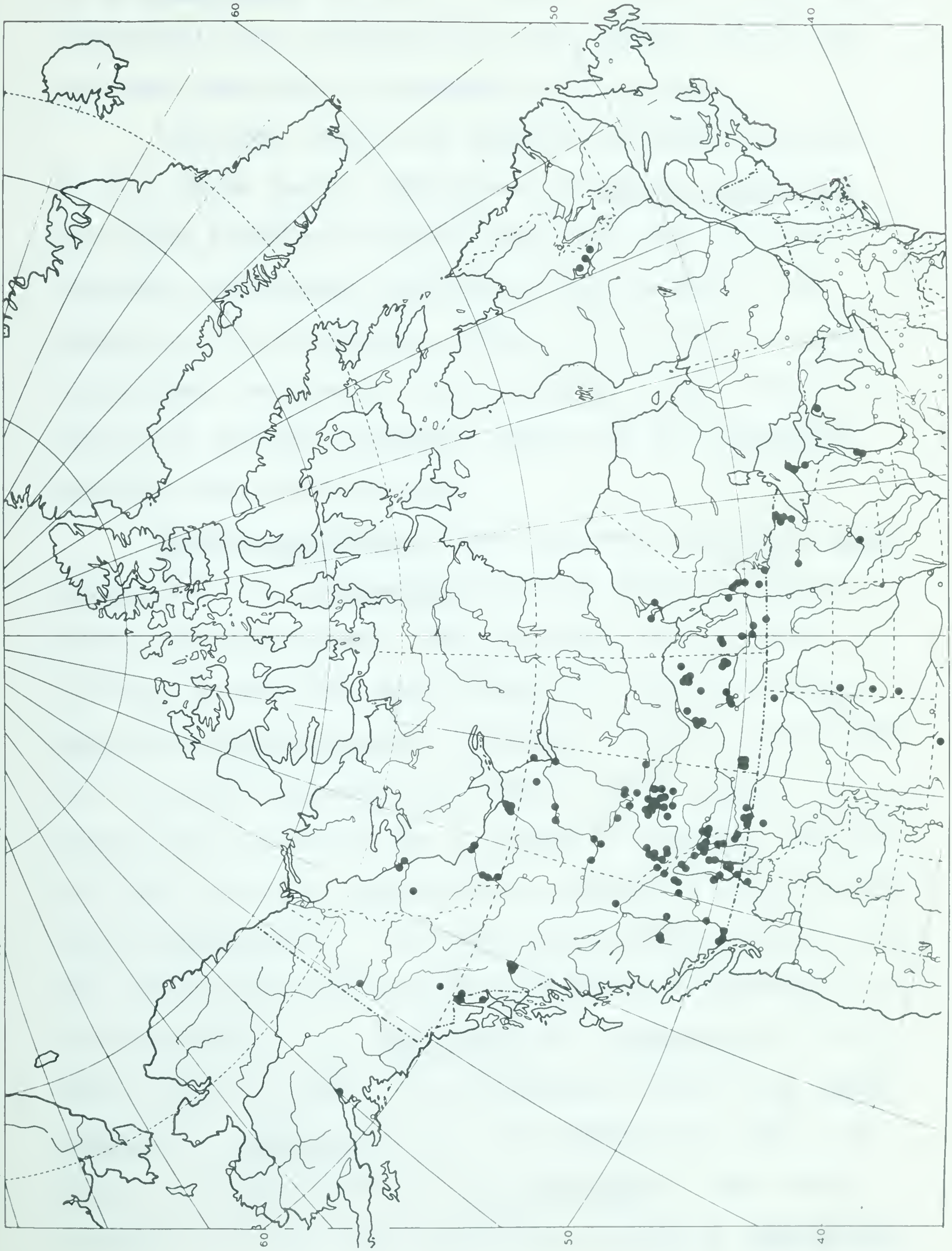
Betula papyrifera is extremely variable and is most easily confused with *B. resinifera* and the two hybrids, *B.* x *utahensis* and *B.* x *winteri*.

It is interesting to note that Johnsson (1945) has reported chromosome numbers of 2n = 70, 71, 72, 75, 77, 80, 82, 83 and 84 for *Betula papyrifera* individuals from Minnesota. Nearly half of these 31 counts were 2n = 84. Clausen (1962, 1963) who apparently did not count the chromosomes of the Minnesota *B. papyrifera*, has reported the number as 2n = 70 or 84, presumably on the basis of Woodworth's earlier counts. The suggestion by Clausen that a chromosome number higher than 2n = 84 might exist

FIGURE 5

Distribution of Betula papyrifera.

(in N.W. North America)


60
50
40
10
20
30
40
60
100
140
160
170
180
170
60
50
40

in _B_. _papyrifera_ (based on a report by Cain, 1953, of an individual with exceptionally large pollen grains) has not been confirmed by Johnsson or the writer.

Johnsson (1945) has reported chromosome numbers of 2n = 70-84 for 83 individuals of _Betula_ _papyrifera_, combining individuals from several origins: British Columbia, Washington, Minnesota, Massachusetts, New Hampshire, New Brunswick, Quebec, and Ontario. A concentration was noted at 2n = 75 and 2n = 84. Table a14 lists the various chromosome counts for _B_. _papyrifera_ found in this investigation.

Betula _papyrifera_ which has been called var. _commutata_ (or var. _occidentalis_) is not distinct and not worthy of recognition. Fernald (1902) has actually referred to the west coast birch with dark bark as _B_. _alba_ forma _occidentalis_. He comments that the dark bark is a variable character and should not be used as a distinctive character for a species or variety, and this has been borne out by subsequent studies of these birches. Other morphological characters and chromosome numbers are not associated with the dark bark which is supposed to be characteristic of _B_. _papyrifera_ var. _commutata_ (Brittain, 1963, 1964, letters). The chromosome number of _B_. _papyrifera_ var. _commutata_ is 2n = 84 (Woodworth, 1931), but this is a common number in _B_. _papyrifera_. Also, many birches with dark bark, suspected of being _B_. _papyrifera_

var. commutata have chromosome numbers of 70. Therefore, at the present time, there is no recognizable distinction between white-barked and dark-barked B. papyrifera, and these are considered color forms.

Representative specimens: BRITISH COLUMBIA: Spanish Banks, Vancouver, W. C. McCalla and J. W. Eastham, 11055 (ALTA); Fraser River, North Bend, W. C. McCalla, 2752 (ALTA); Mara Lake, south of Sicamous, W. C. McCalla, 11463 (ALTA); Kicking Horse River, Yoho National Park, W. C. McCalla, 7567 (ALTA); Mt. Revelstoke, W. C. McCalla, 11456 (ALTA); Kicking Horse River, east of Field, W. C. McCalla, 4567 (ALTA); Alaska Highway, mile 496, A. E. Porsild, 9.070 (GH); Near Falkland, C. L. Hitchcock and J. S. Martin, 7457 (A); Mount of Quartz Creek, H. M. Raup and E. C. Abbe, 4212 (A); Lake, Vancouver Island, J. Macoun, 1 (A); Sidney, Vancouver Island, J. Macoun, June 17, 1914 (GH); 2 miles east of Field, J. R. D., 2016 (ALTA); Thunder Hill Campsite, Columbia Lake, J. R. D., 2338, 2294, 2349 (ALTA); Fernie Campsite, J. R. D., 2280 (ALTA); 2 miles east of Nelson, W. C. McCalla, 8108A (ALTA); 10 miles north of Princeton, J. R. D., 2382, 2383, 2384, 2381 (ALTA); Grindrod, J. R. D., 2385, 2386, 2387 (ALTA); Victor Lake Picnic site, J. R. D., 2388, 2389 (ALTA); Golden, J. R. D., 2390 (ALTA); Lockhart Beach Provincial Park, Kootenay Lake, J. R. D., 2351 (ALTA); Kootenay Lake, J. R. D., 2354, 2355, 2356 (ALTA); Kokanee Creek Provincial Park on west arm Kootenay Lake, J. R. D.,

2357, 2358 (ALTA); Cultus Lake Provincial Park, J. R. D., 2370, 2371, 2372 (ALTA); Frazer Valley, north of Hope, J. R. D., 2373, 2374 (ALTA); Frazer Valley, 6 miles north of Hope, J. R. D., 2375, 2376, 2377 (ALTA); Emory Creek Campsite, J. R. D., 2378, 2379, 2380 (ALTA); Hatzic (C.P.R.), J. G. Jack, 2897 (US); Burgess Trail near Field, S. Brown, 496 (US); Banks of Frazer near Yale, G. Engelmann and C. S. Sargent, July 22, 1880 (A); Hazelton, Skeena River, J. M. Macoun, July 4, 1917 (A); Within 5 miles of Lillooet, J. M. Macoun, July 3, 1916 (A)(US); Crescent, J. H. Henry, Sept. 18, 1914 (A); Within 5 miles of Brackendale, Squamish River, J. M. Macoun, June 12, 1916 (A); Fraser River (bark only) (A); Chilliwack Valley, J. M. Macoun, August 8, 1901; July 21, 1901 (A); Donald, Columbia River, J. Macoun, July 4, 1885 (A); Mainland opposite Vancouver Island, Anderson (bark only) (A); Lost Lake near Victoria, J. Macoun, July 21, 1908 (A); Sumas Lake, Fraser Valley and Chilliwack Valley, J. M. Macoun, August 8, 1901 (A); Sicamous, J. Macoun, July 3, 1889 (MIN); High rocks above Emerald Lake, C. H. Shaw, 584 (US); Revelstoke, J. Macoun, May 5, 1890 and June 24, 1890 (US); South Hazelton, R. Pillsbury, 149 (DAO); Below New and South Hazelton, R. Pillsbury, 154 (DAO); Yale, E. W. Sullivan, S59470 (DAO); Similkameen River near Allenby, A. W. McCallum, 33 (DAO); Locarno Park, Vancouver, J. W. Eastham, (DAO); Tranquille Range, Kamloops, E. W. Tisdale, 40-308 (DAO); Mt. Revelstoke National Park, E. H. Wallis,

28-64 (DAO); Lillooet River, T. R. Ashlee, 24/5/1923 (DAO). ALBERTA: 8 miles west of Gilby, J. R. D., 1309 (ALTA); Botanic Gardens, J. R. D., 1372 (ALTA); North Saskatchewan River bluffs, J. R. D., 1373, 1376, 1380 (ALTA); White Mud Creek Bluff, J. R. D., 1386, 1389 (ALTA); Woods near Gunn on Lac Ste. Anne, J. R. D., 1393 (ALTA); Campsite near Chisholm, J. R. D., 1462, 1463 (ALTA); Campus, University of Alberta, Edmonton, J. R. D., 1478 (ALTA); Sandy soil near Fedora, J. R. D., 1480 (ALTA); 2 miles north of Highway 28, J. R. D., 1536 (ALTA); Beach road, Cold Lake, J. R. D., 1574 (ALTA); Queen Elizabeth Park, Edmonton, J. R. D., 1588 (ALTA); Muir Lake, Edmonton Fish and Game Campground, J. R. D., 1591 (ALTA); Hilltop near Muir Lake, J. R. D., 1595 (ALTA); Hills north of Muir Lake, J. R. D., 1620, 1621, 1622, 1624, 1625a, 1626 (ALTA); Forest near Waterton Townsite, Waterton National Park, J. R. D., 1638, 1639, 1640 (ALTA); Linnet Lake, Waterton National Park, J. R. D., 1661, 1662, 1663, 1664, 1665, 1666, 1667, 1668, 1669, 1670 (ALTA); Cameron Falls, Waterton National Park, J. R. D., 1677, 1678, 1679 (ALTA); Campus, University of Alberta, J. R. D., 1695 (ALTA); Punchbowl Falls near Pocahontas, Jasper National Park, J. R. D., 1735, 1736, 1737 (ALTA); Road to Mt. Edith Cavell, J. R. D., 1744, 1745 (ALTA); Maligne Canyon, Jasper National Park, J. R. D., 1747, 1749 (ALTA); Near Falls on Yellowhead Pass Road, Jasper National Park, J. R. D., 1750 (ALTA); Near entrance to Jasper National Park, J. R. D.,

1766, 1767, 1768 (ALTA); Emily Murphy Park, Edmonton, J. R. D., 1812, 1815, 1817, 1824 (ALTA); Mile #3, Celestine Lake Road, Jasper National Park, J. R. D., 1931, 1933 (ALTA); Cascade Mountain, Banff National Park, J. R. D., 2031, 2032,(ALTA); Elizabeth Park, Edmonton, J. R. D., 2073 (ALTA); Picnic Island, Elk Island National Park, J. R. D., 2090 (ALTA); Hillside above bog near north entrance, Elk Island National Park, J. R. D., 2107 (ALTA); Bluffs of North Saskatchewan River, Edmonton, J. R. D., 2147 (ALTA); Sandhill, Ponoka Bog, J. R. D., 2179 (ALTA); Lac Ste. Anne, A. W. L. Stewart, 2202 (ALTA); Linnet Lake, Waterton National Park, J. R. D., 2278a, 2279a (ALTA); West shore of Waterton Lake, Waterton National Park, A. J. Breitung, 17536 (ALTA); East of Mulhurst on Pigeon Lake, G. H. Turner, 5040 (DAO); River bank, Ft. Vermilion, H. Groh, 2827 (DAO); Astoten Lake, Elk Island, Elk Island National Park, R. D. Ursher, 17-55 (DAO) (MIN); Elk Island, Astoten Lake, Elk Island National Park, R. D. Ursher, 17-53 (MIN) (DAO); Embarrass, M. E. Oldenburg, 40-120 (MIN); South end of Astoten Lake, Elk Island National Park, B. O'Connor, 17-22 (MIN) (DAO); Near Jasper Park Lodge, Jasper National Park, J. G. Jack, 2590 (US); Whistler's Mountain Trail, Jasper National Park, J. G. Jack, 2691 (US); Elk Island, Elk Island National Park, B. O'Connor, 17-20 (US) (DAO) (MIN), 17-21 (MIN); Ft. Fitzgerald, W. J. Cody and C.C. Loan, 4426 (US); Waterton Lake, Waterton

National Park, A. J. Breitung, 16646 (DAO); Widewater, Lesser Slave Lake, E. H. Moss, 7388 (DAO); Big Island, Lac la Biche, W. J. Cody and R. L. Gutteridge, 7066 (DAO); Lac la Biche, W. J. Cody and R. L. Gutteridge, 6959 (DAO); Fort Saskatchewan, G. H. Turner, 5805 (DAO); North east of Fort Saskatchewan, G. H. Turner, 2484 (DAO).

SASKATCHEWAN: 4 miles west of McKague, A. J. Breitung, 635 (DAO); Qu'Appelle Valley, B. de Vries, 335 (DAO); Cypress Hills, Birch Creek Ranger Station, A. J. Breitung, 4823, 4821, 4379 (DAO); Cypress Hills, Fort Walsh, A. J. Breitung, 5247 (DAO); 11 miles S.W. of McKague, A. J. Breitung, 391 (DAO); Moose Mountain Forest Reserve, J. B. Campbell, August, 1949 (DAO); Cornwall Bay, Lake Athabaska, H. M. Raup, 6601 (GH); Wolverine Point Lake Athabaska, H. M. Raup, 6835 (GH); 11 miles S.W. of McKague, A. J. Breitung, 391 (DAO); Bank above river, St. Louis, H. A. Senn, H. Groh, R. C. Russell, 2863 (DAO); S.W. of McKague, A. J. Breitung, 183 (DAO) (US); N.E. of Wallwort, A. J. Breitung, 575, 576 (DAO); Saskatoon, 18 miles south, G. F. Ledingham, 48-135 (DAO); 4 miles south of McKague, A. J. Breitung, 183 (DAO) (US); west of St. Victor, H. A. Senn, 2459 (DAO); Hudson Bay Junction, north shore of Red Deer River, A. J. Breitung, 995 (DAO); Saskatoon, R. C. Russell, 2800 (DAO).

MANITOBA: Gimli, M. G. Dudley, 1939 (DAO); 175 miles N.E. of Winnipeg, A. J. Breitung, 7545 (DAO); Riding Mountain National Park, J. S. Rowe, 316 (DAO); Forestry camp, Riding

Mountain National Park, J. S. Rowe, 315 (DAO); Brandon, H. H. Marshall, 30 (DAO); Indian Bay, M. G. Dudley, 72 (DAO); 8 miles west of Norgate, A. and D. Löve, 6562 (DAO); Camp Morton, A. and D. Löve, 5725 (DAO); Morden, H. Groh, August 19, 1922 (DAO); S.E. of Middlebro, A. and D. Löve, 6144 (US); west of Ninette, A. and D. Löve, 6037 (US).

QUEBEC: Baie d'Ungava, A. Dutilly and E. Lepage, 39420 (DAO); Baie d'Ungava, A. Dutilly and E. Lepage, 39033 (DAO); Sainte-Genevieve, Ile Mallette, F. Marie-Victorin, 21 731 (GH); Thetford, Co. de Megantic, F. Marie-Victorin, 11 185 (GH).

NORTHWEST TERRITORIES: Lagoon, Lower Hay River, W. H. Lewis, 952 (DAO); Enterprise-Mackenzie River Highway, mile 20, J. W. Thieret and R. J. Reich, 4889 (US)(DAO); Enterprise-Mackenzie River Highway, mile 64, J. W. Thieret and R. J. Reich, 5071 (US)(DAO); Enterprise-Mackenzie River Highway, Kakisa River near ford, J. W. Thieret and R. J. Reich, 4781 (DAO); Enterprise-Mackenzie River Highway, mile 25, J. W. Thieret and R. J. Reich, 4942 (US)(DAO); Mackenzie River opposite Fort Simpson, W. J. Cody and J. M. Matte, 8488 (DAO); 3 miles S.E. of Fort Simpson, W. J. Cody and J. M. Matte, 9235 (DAO); Fort Liard, W. J. Cody and K. W. Spicer, 11755 (DAO); 15 miles north of Fort Liard, W. J. Cody and K. W. Spicer, 11841 (DAO).

ALASKA: Skagway, M. O. Malte, 273 (GH).

WASHINGTON: Cascade Mountain, J. M. Grant, May, 1927 (A);

Milan, Spokane Co., J. G. Jack, 1468 (A); Northwest Washington, C. V. Piper, 1892 (A); Eversons, Whatcom Co., C. V. Piper, 1128 (A); Near Spokane, Spokane Co., E. J. Palmer, 37842 (A); Newhalem, A. L. Haines, 8505 (A); Everson, Whatcom Co., C. V. Piper, 1128 (GH); Whatcom Co., Mount Baker at Belle Creek, G. Turesson and C.G. Alm, 787 (GH); 12 miles south of Pullman, C. V. Piper, 3574 (GH); Eastern Washington, W. B. Ayers, CXXX (A).

OREGON: Umatilla Co., along Umatilla River near Bingham Springs, W. C. Cusick, 3267 (DAO).

IDAHO: Idaho Co., near Selway River, Marion Ownbey and G. H. Ward, 3128 (DAO); Midas, E. C. Jahn and E. R. Martell, 8362 (A); Priest River Station, C. S. Sargent, July 29, 1896 (A); Sandpoint, J. G. Jack, 1496 (A); Foothills, Latah County, A. D. E. Elmer, 194 (A).

MONTANA: Columbia Falls, J. G. Jack, 1573 (A); Kalispell, J. G. Jack, 1611 (A); Lake McDonald, Glacier National Park, J. G. Jack, 2277 (A); Lake McDonald, F. W. Hunnewell, 2384 (GH).

NORTH DAKOTA: Metigoshe State Park, O. A. Stevens, 2056, 2055 (DAO).

SOUTH DAKOTA: Deadwood, W. P. Carr, 34 (DAO); Spearfish, Lawrence Co., F. L. Bennett, 90 (DAO); Pennington Co., ravines near Hill City, C. L. Porter, 6598 (DAO).

NEBRASKA: Harrison, J. M. Bates, Aug. 22, 1890 (GH).

MINNESOTA: Mille Lacs Co., Rum River south of Onamia, J. W.

J. W. Moore and N. L. Huff, 19588 (DAO); Namaskan Lake terrace at Kettle Falls, St. Louis Co., Olga Lakela, 13230 (DAO); Benedict, H. F. Bergman, 3010 (DAO); St. Louis Co., river bank, Olga Lakela, 19918 (DAO); Rainy Lake, international boundary, Olga Lakela, 14641 (DAO); St. Louis County, Namakan Narrows, Olga Lakela, 14205 (DAO); Curtain Falls, St. Louis Co., Olga Lakela, 11463 (DAO); 5 miles from the Narrows, St. Louis Co., Olga Lakela, 14319 (DAO); Itasca Park, M.G. Dudley, May 31, 1932 (DAO); Le Sueur Co., K. Clausen, 75 (DAO).

WISCONSIN: Devil's Lake, Sauk Co., M. N. Zinck, 608 (DAO); Manitowoc Co., J.A. Reed, 717, 696 (DAO).

MICHIGAN: Cheboygan Co., 6 miles N.W. of Topinabee, L. H. Shinners, 13752 (DAO); Shore of Smoky Lake, Iron Co., C. D. Richards, 3488 (DAO); Mt. Brockway, Keewinaw Peninsula, W. G. Dore, 10434 (DAO); Houghton Co., Jacobsville Quarry, C. D. Richards, 3628 (DAO).

MAINE: Deer Isle, W. C. Appleton, August 23, 1925 (GH).

BETULA X ULIGINOSA n. 'sp.' hyb.

Betula pumila var. glandulifera Regel x B. resinifera Britton

Frutex magnum, 1-5 m procerum, erectum et expandens. Ramuli spadices cum magnis glandibus sufflavis resinosis splendentibus. Cortex non-exfolians fuscus. Folia late ovata, acute ad anguste rotundus apud apicem, crenata-serrata ad inaequaliter et late serrata, ferme 15-25 serrationes in margine uno, cum fundamento rotundato ad cuneatum, 3-5 cm longo 2-3.5 cm lato. Amenta pistillata in fructo 2-2.5 cm longa, 7-9 mm lata, in pedunculis 1-2 cm longis, cylindricis obtusis habentibus bracteas ut solet latioras quam longas et lobos laterales plerumque obtusa cum longiore lobo medio rotundo-acuto. Corpus samerae ovatum ad obovatum, 2-3 mm longum 1-2 mm latum non angustius quam ala. Numerus chromosomorum 2n = 28-56.

Shrub, 1-5 m tall, usually several trunks present, erect and spreading; branchlets reddish brown, glabrous, covered with large, lustrous, yellowish resinous glands. Bark not exfoliating, brown, usually shining. Winter-buds acute, brown, resinous. Leaves broadly ovate, acute to narrowly rounded at the apex, crenate-serrate to irregularly broadly serrate, usually 15-25 serrations on one margin, rounded to cuneate base, glabrous, dark green above, pale below, becoming rusty-yellow in autumn, 3-5 cm long, 2-3.5

cm wide, reticulate, veinlets more conspicuous on lower surface, with multicellular peltate glands on both leaf surfaces, stomata averaging 21-38 μ; petioles slender, reddish, glabrous, glandular, 10-15 mm long. Staminate catkins usually solitary or in pairs, sessile, 1-2 cm long during the winter, elongating to 3-4 cm in spring, bracts ovate, pubescent, dark brown, pale and ciliate on the margin, rounded acute at the apex, pollen averaging from 18-27 μ in diameter. Pistillate catkins 1 cm long in flower, in fruit erect or pendulous, 2-2.5 cm long, 7-9 mm wide, on peduncles 1-2 cm long, cylindric, obtuse, bracts usually broader than long, lateral lobes mostly obtuse with longer middle lobe rounded-acute. Body of samara ovate to obovate, 2-3 mm long, 1-2 mm wide, as wide as wing. Chromosome number 2n = 28-56.

Types: Holotype: Ponoka bog, 71 miles south of Edmonton, Alberta, Janet R. Dugle, 1689A, August 13, 1961 (ALTA). (See Plate a5).

Isotype: Ponoka bog, 71 miles south of Edmonton, Alberta, Janet R. Dugle, 1689b, July 10, 1963 (ALTA).

Distribution: Bogs and sandhills of central Alberta.

Representative specimens: ALBERTA: Ponoka bog, 71 miles south of Edmonton, J. R. D., 1691, 1698, 1700, 1701, 1703, 1704, 1705, 1706, 1709, 2159, 2161, 2172, 2174, 2176,

2178, 2212, 2217, 2218, 2305, 2313, 2314, 2315 (ALTA); Near Wizard Lake, J. R. D., 1300 (ALTA); Bog on highway 43, 1 mile from Sangudo, J. R. D., 1401 (ALTA).

<u>BETULA</u> X <u>SARGENTII</u> n. 'sp.' hyb. , n.m. <u>SARGENTII</u>

<u>Betula</u> <u>pumila</u> var. <u>glandulifera</u> Regel x <u>B</u>. <u>glandulosa</u> Michx.

<u>Frutex, idem suo more et duae parentum species. Ramuli tecti aut magis aut minus glandibus sufflavis resinosis. Cortex suffuscus, non-exfolians. Folia elliptica 2-2.5 cm longa, 15-18 mm lata, crenata, cum 10-15 crenationibus praeter utrumque marginem. Amenta pistillata in fructu 1-2 cm longa, 6-10 mm lata, ovoida ad anguste cylindrica cum lobis bractearum digredientibus, rotundis apud apices et lobis lateralibus paeve aeque longis cum lobo medio. Corpus samerae ovatum usque ad orbiculare, 1-2 mm longum, 1-2 mm latum, multo latius quam ala. Numerus chromosomorum 2n = 28-56</u>.

Shrub, 5-30 dm tall, having the general habit characteristics of the two parental species; branchlets usually slender, reddish brown, more or less covered with scattered yellowish resinous glands. Bark dark brown, dull. Leaves dark green and shining above, usually pale below, turning rusty yellow to reddish in autumn, usually elliptic, 2-2.5 cm long, 15-18 mm wide, round-cuneate at the base, crenate, usually 10-15 crenations along each margin, glandular dotted below, pubescent on the veins when young, finely reticulate, with peltate multicellular glands sparsely arranged on the upper leaf surface; stomata averaging from 20-34 μ; petioles yellowish to reddish, smooth, pubescent.

Staminate catkins 4-10 mm long during the winter, with ovate, dark green glandular bracts, the catkins becoming 10-20 mm long at anthesis; pollen averaging from 16-25 μ in diameter. Pistillate catkins about 10 mm long in flower; in fruit 10-20 mm long, 6-10 mm wide, ovoid to narrow cylindrical, lobes of bracts divergent, rounded at the apices, lateral lobes nearly as long as the middle lobe. Body of samara ovate to orbicular, 1-2 mm long, 1-2 mm wide, much wider than the wing. Chromosome number $2n = 28\text{-}56$.

Types: Holotype: Campsite near Obed, Alberta, Janet R. Dugle, 1723, September 5, 1961 (ALTA). (See Plate a7).

Distribution: Areas in which the two parental species are in contact; western Alberta in the foothills and mountains east to Saskatchewan, Manitoba and Ontario; north in Northwest Territories in bogs.

Taxonomic Notes: *Betula x sargentii* hybridizes with: *B. papyrifera* (*B. x arbuscula*); see page 107, 200.

This birch was named for Charles Sprague Sargent (1841-1927), outstanding North American taxonomist, who contributed much to the knowledge of the genus *Betula*.

Betula x sargentii is a very important member of the flora in western Alberta. It has been a source of confusion because of its intermediate characteristics. Detailed analyses of these populations are presented beginning on page 159.

<u>Representative specimens</u>: BRITISH COLUMBIA: Beaton River Crossing, T. M. C. Taylor, A. Szczawinski and M. Bell, 45 (DAO); McLatchie Lake, Flathead, M. Bell and J. Davidson, 938 (DAO); Bennett, D. A. Mitchell, 167 (DAO); Burgess Pass, F. Fyles, Aug. 31, 1914 (DAO); Emerald Lake, H. Petersen, 97 (MIN); Paul Creek, Ashnola Range, south of Hedley, G. Beke, Sept. 11, 1960 (DAO).

ALBERTA: Lake Louise, Herman von Schrenk, August 2-3, 1921 (MIN); Bow River, Calgary, J. Macoun, June 5, 1897 (CAN); Ma-Me-O Beach on Pigeon Lake, G. H. Turner, 5943 (CAN); 1 mile southwest of Ft. Smith, W. J. Cody and C. C. Loan, 3606 (MIN), 3681 (US); Basin, Banff, S. Brown, 4 (MIN) (US); Bog on Red Deer-Nordegg road, 3 miles west of Rocky Mountain House, F. J. Hermann, 13301 (US); Bow River Valley, Banff, W. C. McCalla, 2383 (US); Waterton Lakes Park, S. S. Survey 655 (ALTA); Banff, F. J. Lewis, June, 1915 (ALTA); Bog near Leslieville, J. R. D., 1318, 1319, 1320, 1321 (ALTA); 6 miles past Rocky Mountain House, bog, J. R. D., 1328 (ALTA); 19 miles west of Rocky Mountain House, J. R. D., 1330 (ALTA); Campsite near Edson, J. R. D., 1720, 1722 (ALTA); Campsite near Obed, J. R. D., 1724, 1725, 1726, 1727, 1728, 1729, 1730, 2237, 2238, 2239 (ALTA); Pyramid Lake, Jasper National Park, J. R. D., 1755, 1752 (ALTA); 4 miles west of Wildwood campsite, J. R. D., 1857, 1858, 1859, 1860, 1861, 1862, 1863 (ALTA); 18 miles west of Wildwood campsite, J. R. D., 1867, 1869 (ALTA); Coalbranch road, 23 miles S.W. of Edson, J. R. D.

1874, 1878, 1882, 1884 (ALTA); Geraldine Lake Road, Jasper National Park, J. R. D., 1949, 1950, 1951, 1952 (ALTA); Jonas Creek Campground, Jasper National Park, J. R. D., 1956 (ALTA); Campsite, Jasper National Park, J. R. D., 1970, 1972, 1974, 1975, 1976, 1977, 1980, 1981, 1982, 1984, 1986, 1987, 1988 (ALTA); Lower Waterfowl Lake, Banff National Park, J. R. D., 1991, 1992, 1996 (ALTA); Bow Lake, J. R. D., 2011 (ALTA); Paradise Creek, J. R. D., 2013, 2014 (ALTA); Mile 12, Fire road in Banff, J. R. D., 2057, 2058, 2059, 2060, 2061 (ALTA); Mile 10, Fire road in Banff, J. R. D., 2062 (ALTA); Kananaskis road to Coleman, 16 miles inside gate, J. R. D., 2261 (ALTA); Boulton Creek, Kananaskis road, J. R. D., 2263, 2264 (ALTA); Cataract Creek, Kananaskis road, J. R. D., 2265, 2266, 2267 (ALTA); Livingstone Falls Campsite, Kananaskis road, J. R. D., 2268, 2269, 2270 (ALTA); Campsite, 3 miles south of Livingstone Falls, Kananaskis road, J. R. D., 2271, 2272 (ALTA).

SASKATCHEWAN: S. E. Grove Lake, G. W. Scotter, 436 (DAO); South shore of Lake Athabasca, G. W. Argus, 262-62, 265-62 (SASK).

MANITOBA: Knife Lake, 120 miles S.W. of Churchill, J. M. Gillett, 2284 (DAO); Gillam, W. Krivda, G-75 (DAO); Churchill H. Ellis, 1290 (DAO); Fort Churchill, W. G. Dore, 9937 (DAO); Churchill, A. H. R. Buller, August 13, 1939 (DAO); W. N. Denike, A-12 (DAO); Beulah, A. J. Dennis, 1621 (DAO).

ONTARIO: Between Thunder Bay and Provincial Paper Mills,

Current River, Port Arthur, C. E. Garton, 2539 (DAO); Moose Factory, D. B. O. Savile, 108 (DAO); Orient Bay, 4 miles south of MacDiarmid, C. E. Garton, 7998 (DAO); 3 miles south of Cooke Point, Lake Nipigon, C. E. Garton, 7716 (DAO).

NORTHWEST TERRITORIES: Along Kakisa lake road, about 1½ miles below Lady Evelyn falls, J. W. Thieret and R. J. Reich, 4573 (US); Hearne Lake, south tip, G. W. Scotter, 908 (DAO); Nahanni Mountains, Mackenzie, E. A. Preble and M. Cary, 74 (US); Fort Good Hope, Mackenzie, E. A. Preble, 337 (US); Yellowknife, W. J. Cody and J. B. McCanse, 2116 (US); 24 miles south of Lower Hay River, W. H. Lewis, 942 (DAO).

YUKON TERRITORY: Dawson, A. Eastwood, 339 (CAN); Mile 95, Canol Road, A. E. Porsild and A. J. Breitung, 10.471A, 10.452 (US)(CAN); Watson Lake, J. M. Gillett, 3565 (DAO).

<u>BETULA</u> X <u>EASTWOODAE</u> Sargent, Man. of the Trees of N. Am., 208 (1905)

<u>Betula</u> <u>glandulosa</u> Michx. x <u>B</u>. <u>fontinalis</u> Sarg.

<u>B</u>. <u>eastwoodae</u> Sargent, Bot. Gaz. 67:216 (1919); Man of the Trees of N. Am., 1:219 (reprinted in 1962)

<u>B</u>. x <u>eastwoodae</u> Sarg. in Anderson, Fl. of Alaska IV: 219, Fig. 368, 369 (1942), (= <u>B</u>. <u>glandulosa</u> x <u>resinifera</u>); in Hultén, Fl. of Alaska and Yukon 4:575 (1944), (= <u>B</u>. <u>glandulosa</u> x <u>resinifera</u>); in Krüssmann, Handbuch der Laubgehölze, Band I: 231 (1962), (= <u>B</u>. <u>glandulosa</u> x <u>papyrifera</u> var. <u>humilis</u>).

<u>B</u>. <u>occidentalis</u> Hook. <u>sensu</u> Raup, National Mus. of Canada Bull. No. 121: 153 (1951), in part.

Large, thicket-forming shrub, 1-7 m tall, usually several trunks present, up to 3 dm in diameter, branches ascending, spreading, branchlets slender, glabrous and covered with persistent, lustrous, yellowish resinous glands. Bark not exfoliating, brown, marked by brown to white lenticels. Winter-buds ovoid, acute, chestnut-brown, 2-3 mm long. Leaves broadly-ovate to elliptic, acute, rounded or abruptly short-pointed at apex, crenate-serrate to serrate, usually 15-25 serrations on one margin, rounded to cuneate base, glabrous, dark green above, pale below, becoming rusty-yellow in autumn, 2-4 cm long, 1.5-3 cm wide, reticulate, veinlets more conspicuous on lower surface,

stomata averaging 22-28 μ petioles slender, glabrous, 5-10 mm long; stipules scarious, ovate-oblong, rounded at the apex. Staminate catkins usually solitary or in pairs, sessile, 1-2 cm long during the winter elongating to 2-3 cm in spring, bracts pubescent, dark red, acute and apiculate at apex, pollen averaging from 19-21 μ in diameter. Pistillate catkins 1 cm long in flower, in fruit pendulous, 1.5-2 cm long, 7-8 mm wide, on peduncles about 1 cm long, cylindric, bracts glabrous, longer than broad, lobes narrowed at the rounded apex, ciliate, the lateral slightly spreading, shorter than the middle lobe. Fruit a samara, body 1.5-2 mm long, 1-1.5 mm wide, usually obovate, puberulent at apex, wider than its wing. Chromosome number 2n = 28.

Types: Isotype: Dawson, Yukon Territory, Alice Eastwood, 271-88, June 17, 1914 (US). (See Plate a8).

Distribution: Marshes and thickets in mountains and northern areas; Alberta and north into Mackenzie District, Northwest Territories, Yukon Territory and Alaska.

Representative specimens: ALBERTA: Campground, 21 miles west of Rocky Mountain House, J. R. D., 1331 (ALTA); Woods, 23 miles S.W. of Edson on Coalbranch Road, J.R.D., 1872, 1875 (ALTA); Lambert Creek campground on Coalbranch Road, J. R. D., 1891 (ALTA); 38 miles S.W. of Edson on Coalbranch Road, J. R. D., 1895, 1897, 1900, 1901

(ALTA); Point of interest sign inside north entrance to Jasper National Park, J. R. D., 1906, 1907, 1908, 1915 (ALTA); Vermilion Lakes, Banff National Park, J. R. D., 2025, 2030 (ALTA).

SASKATCHEWAN: East arm of Offset Lake, G. Scotter, 468, 454 (DAO).

NORTHWEST TERRITORIES: Just below summit of Mount Coty, W. J. Cody and K. W. Spicer, 11804 (DAO); East bank of east channel Mackenzie River, W. J. Cody and D. H. Ferguson, 10370 (DAO); "Burnt Lake", Eskimo Lake Basin, W. J. Cody, 10130 (DAO); Aklavik, Mackenzie River Delta, W. J. Cody and R. L. Gutteridge, 7926 (DAO); Mackenzie River-Rae Highway, 16 miles north of Mackenzie River, J. W. Thieret and R. J. Reich, 5035 (DAO); Vicinity of Lake-on-the-Mountain, J. W. Thieret and R. J. Reich, 5930 (DAO); Indin Lake, W. J. Cody and J. B. McCanse, 3442 (DAO); Port Radium, Eldorado Mine, W. J. Cody, 2796 (DAO); Yellowknife, W. J. Cody, 2525 (US) (DAO); Great Bear Lake, north shore of McTavish Arm, A. E. and R. T. Porsild, 5229 (US); Unnamed lake, 62°55'N., 111° 55'W, G. W. Scotter, 1062 (DAO); Lagoon, Lower Hay River, W. H. Lewis, 954 (DAO); Eskimo Lake Basin, southeast of Setidgi Lake, A. E. and R. T. Porsild, 3143 (US).

YUKON TERRITORY: Sulphur Creek S.E. of Dawson, J. Terasmae (DAO); Dawson, Alice Eastwood, 282, 433 (US); Klondike Indian Divide, J. Macoun, August 15, 1902 (US); Roadside

Hunker Creek, J. Macoun, August 4, 1902 (US); Hunker Creek, J. Macoun, July 23, 1902 (US); Fort Good Hope, Mackenzie, E. A. Preble, 336 (US); Canol Road, mile 132, A. E. Porsild and A. J. Breitung, 9.604 (US); Bear Creek area about 8 miles east of Dawson, J. A. Calder and L. G. Billard, 3025 (US).

BETULA X UTAHENSIS Britton, Torrey Bot. Club Bull. 31: 165 (1904), *pro sp*.

B. fontinalis Sarg. x *B. papyrifera* Marsh.

B. utahensis Britton, N. Am. Trees 254 (1908); Butler, Torrey Bot. Club Bull. 36: 432, Fig. 11 (1909).

B. andrewsii Nelson, Bot. Gaz. 43: 279-281 (1907), *nomen provisiorum*; Coulter, Rev. by Nelson, New Man. of Botany of Central Rocky Mountains (1909).

B. papyrifera andrewsii (A. Nels.) Daniels, Flora of Boulder, Colo., and Vicinity, Univ. of Mo. Studies, Science Series Vol. 2, No. 2 (1911).

B. x *andrewsii* Nelson *sensu* Froiland, Evolution 4: 268-282 (1952)

B. subcordata Rydberg in Butler, Torrey Bot. Club Bull. 36: Fig. 15 (1909).

B. papyrifera var. *subcordata* (Rydb.) Sargent, Journ. Arnold Arb. 1: 63 (1919), in part; Man. of the Trees of N. Am., Vol. I: 214, Fig. 201 (1905), reprinted 1962, in part; Abrams, Illustrated Flora of the Pacific States Vol. I: 512 (1940), in part; Davis, Flora of Idaho, 237 (1952), in part; Breitung, Am. Midland Naturalist 58: 25 (1957), in part; Moss, Flora of Alberta, 185 (1959), in part; Krüssmann, Handbuch der Laubgehölze, Band I: 236 (1962) in part.

B. papyrifera Marsh. *sensu* Rydberg, Flora of the Prairies and Plains, 260 (1932) in part: *sensu* Harrington, Man. of the Plants of Colorado 180 (1954).

B. x *conmixta* Sargent, Man. of the Trees of N. Am., Vol. I: 218 (1905), reprinted 1962.

B. *glandulosa* x *resinifera* - *B*. *conmixta* Sarg. *sensu* Hultén, Flora of Alaska and Yukon 4: 575 (1944) in part.

B. *montanensis* Butler, Torrey Bot. Club Bull. 36: 438, Fig. 17 (1909).

B. *papyrifera* var. *montanensis* (Butler) Sargent, Jour. Arn. Arb. 1: 63 (1919), in part; Man. of the Trees of N. Am. Vol. I: 214, Fig. 202 (1922), reprinted 1962, in part.

Small tree or large shrub, 8-15 m tall, usually several trunks present, up to 5 dm in diameter, branches ascending and spreading; branchlets somewhat glandular, glabrous, red-brown or greenish brown and shining. Bark somewhat exfoliating, brown to orange and silvery yellow, often very lustrous. Leaves ovate to broadly ovate, mostly acute at the apex, truncate, rounded or cuneate at the base, margin serrate to doubly-serrate; green, turning yellow in autumn; pubescent when young to glabrous, 3.5-6 cm long, 3-5 cm wide; stomata averaging 27-34 μ; petioles 1-2 cm long, sparingly pubescent or glabrous and sparsely glandular. Staminate catkins 1-3, clustered, 10-20 mm long during the winter elongating to 50 mm long or longer in the spring, bracts ovate, brownish green, with pale ciliate margins; pollen averaging from 24-26 μ in diameter.

Pistillate catkins about 15 mm long in flower, in fruit cylindric, 20-40 mm long, 5-10 mm wide, erect or pendulous on peduncles 6-20 mm long; their bracts puberulent, ciliate, lobes divergent, the middle lobe acute, rather longer than the broad truncate lateral lobes. Fruit a samara, body 2-3 mm long, 1-2 mm wide, obovate, narrower than its wings. Chromosome number 2n = 28-84.

Types: Holotype: Salt Lake City, Utah, City Creek Canon, April 18, 1900, S. G. Stokes (NY). There are two specimens on the type sheet; the younger must have been collected at the above date, but the other specimen is in fruit and could not have been collected on that date. (See Plate a9).

Distribution: Common where the parental species occur together; especially mountains in British Columbia, Alberta; north into the Yukon and south to Colorado, Idaho, Utah, and Montana.

Taxonomic Notes: In section II (page185) details of various techniques applied to these birches are given. Type specimens of the various birch taxa were analyzed together with the birches collected in Thunder Hill and Celestine Lake. It was found that these birches, *Betula* x *andrewsii* (Plate a10), *B. utahensis* (Plate a9), *B.* x *conmixta* (Plate a11), *B. montanensis* (Plate a12), and *B. subcordata* (Plate a13), were hybrids of *Betula fontinalis* x *B. papyrifera* as had been shown by Froiland (1952) in the case of *B.* x *andrewsii*. The name which has priority

is _B_. _utahensis_, and this name has therefore been applied to this hybrid taxon. It is suggested that this hybrid is a possible origin for some of the reported paper birches with 2n = 56 chromosomes.

Representative specimens: BRITISH COLUMBIA: Thunder Hill campsite, Columbia Lake, J. R. D., 2326, 2327, 2328, 2329, 2335, 2336, 2337, 2332, 2333, 2334, 2296, 2330, 2331, 2339, 2341, 2342, 2343, 2344, 2345, 2346, 2347, 2348, 2340, 2291, 2295, 2293, 2288, 2289 (ALTA); Hazelton, Skeena River, J. M. Macoun, July 14, 1917 (US); Quesnal dam, W. A. Newcombe, Aug. 19, 1917 (GH); Glacier, Selkirk Mountains, F. K. Butters, 731 (MIN); Bank of West Arm of Kootenay Lake east of Nelson, W. C. McCalla, 8108A (ALTA); Valley near Kelowna, W. C. McCalla, 11565 (ALTA); Within 5 miles of Lilooet, J. M. Macoun, July 5, 1916 (A); Wooded bank of Kicking Horse River, east of Field, W. C. McCalla, 4567 (ALTA); Field, J. G. Jack, Sept. 7, 1907 (A); West arm of Kootenay Lake, 2 miles east of Nelson, 8108 (ALTA); Richter Pass Road, above Osoyoos, K. Beamish, F. Vrugtman, and E. Kallio, 9030 (DAO); Between Yellowhead Pass Road and Kinney Lake, L. Jenkins, 7130 (DAO); Boundary Creek campsite, 2359, 2360, J. R. D. (ALTA); Simulkameen River, Bromley Picnic site, J. R. D., 2361 (ALTA); Sicamous, J. Macoun, July 3, 1889 (MIN) (A); Vicinity mouth of Quartz Creek, H. M. Raup and E. C. Abbe, 4212 (MIN); West Branch Gold River, F. K. Butters, E. W. D. Holway, 510 (MIN).

ALBERTA: North shore of Devil's Head Lake, near Banff, W. C. McCalla, 2386 (US); Celestine Lake Road, Jasper National Park, J. R. D., 1940, 1941, 1942, 1934, 1943, 1944, 1945, 1946, 1929, 1930, 1932, 1947, 1948 (ALTA); Crow's Nest Pass, J. Macoun, 18,352 (A).

YUKON: 24 mile house, Dawson, A. Eastwood, 367 (Isotype of B. x conmixta Sargent) (US) (See Plate a11).

WASHINGTON: Blue Mountains, C. S. Sargent, July 31, 1896 (A); Scotia, J. G. Jack, 1481 (A); Ahuota, C. V. Piper, 1642 (A); Blue Mountains, Walla Walla Co., C. V. Piper, July 17, 1896 (A).

OREGON: Along Minam River, E. P. Sheldon, 8746 (A); Blue Mountains, W. C. Cusick, 3616 (GH).

IDAHO: Copses at Hope, Kootenai County, J. H. Sandberg, D. T. MacDougal, A. A. Heller, 1024 (GH); Sandpoint, L. F. Henderson, 2982 (GH); Along Hatwai Creek, Nez Perces Co., J. H. Sandberg, D. T. MacDougal, and A. A. Heller, 33 (A) (Type of B. subcordata Rydb.) (See Plate a13).

MONTANA: Lake McDonald, Glacier National Park, J. G. Jack, 2282 (A); Kalispell, J. G. Jack, 1567, 1557, 1614, 1610, 1615, 1616 (A); Big Fork, vicinity of Flathead Lake, J. Clemens, July 18, 1908; July 15, 1908 (A); Arlee, about 3 miles up Jocko, J. E. Kirkwood, 1080 (GH); Yellow Bay, Flathead Lake east, B. T. Butler, 360 (NY) (Type of B. montanensis Butler) (See Plate a12); Yellow Bay, Flathead Lake east, B. T. Butler, 359 (Marked "cotype" of B. montanensis Butler) (NY).

WYOMING: Crook Co., Bear Lodge Range between Alva and Aladdin, C. L. Porter and M. W. Porter, 7835 (DAO). COLORADO: Boulder Co., ravine northwest of Green Mountain, southwest of Boulder, W. A. Weber, 4924 (DAO) (specimen collected from type tree of _B_. x _andrewsii_ Nelson); Long Canyon near Boulder, Boulder Co., W. A. Weber, 4,3,1,6, 5 (COLO); Long Canyon near Boulder, Boulder Co., W. A. Weber, 7 (specimen collected from type tree of _B_. x _andrewsii_ Nelson) (COLO) (See Plate a10).

BETULA X ARBUSCULA n. 'sp.' hyb.

Betula x *sargentii* Dugle x *B. papyrifera* Marsh.

Frutex magnum 2-8 m procerum cum ramis ascendentibus et expandentibus. Ramuli fere non gladifri, subvirid-fusci, glabri, fulgentes. Cortex non-exfolians, fuscus. Folia ovata ad elliptica plerumque acuta apud apicem apud fundum cuneata cum serrato margine, 3-5 cm longa, 2-3 cm lata. Amenta pistillata in fructu cylindrica 1.5 cm longa, 10 mm lata, erecta in pedunculis 5 mm longis; eorum bracteae puberulentae, ciliatae, habentia lobos ascendentes lobis lateralibus apud apicem rotundis et lobo medio acuto et longiore quam lateralibus lobis. Samerae corpus 1-2 mm longum 1-2 mm latum, latius quam ala. Numerus chromosomorum $2n = 28 - 84$.

Large shrub, 2-8 m tall, usually several trunks present, up to 2 dm in diameter, branches ascending and spreading; branchlets usually not glandular, greenish brown, glabrous, shining. Bark not exfoliating, brown, often very lustrous. Leaves ovate to elliptic, mostly acute at the apex, cuneate at the base, margin serrate; green, turning yellow in the autumn; mostly glabrous, 3-5 cm long, 2-3 cm wide; multicellular peltate glands located sparingly on both leaf surfaces; stomata averaging 29-52 μ; petioles 5-15 mm long, sparingly pubescent or glabrous and sparsely glandular. Staminate catkins 1-2, clustered,

1-1.5 cm long during the winter elongating to 5 cm long in the spring, bracts broadly ovate, pubescent, dark brown-green, reddish at the margin, acute at the apex; pollen averaging from 21-39 μ in diameter. Pistillate catkins about 1 cm long in flower, in fruit cylindric, 1.5 cm long, 1 cm wide, erect on peduncles 5 mm long; their bracts puberulent, ciliate, lobes ascending, lateral lobes round at the apex, middle lobe acute, longer than the lateral lobes; body of samara 1-2 mm long, 1-2 mm wide, wider than the wing. Chromosome number 2n = 28 - 84.

Types: Holotype: Mountain Creek at Pocahontas, Jasper National Park, September 5, 1961, Janet R. Dugle, 1734 (ALTA). (See Plate a13).

Isotype: Mountain Creek, Pocahontas, Jasper National Park, August 28, 1962, Janet R. Dugle, 2240 (ALTA).

Distribution: Apparently rare, found only in disturbed areas in Jasper National Park, Alberta.

Representative specimens: ALBERTA: Milepost #3, Miette Hot Springs Road, Jasper National Park, J.R.D., 1731, 1732; Road to Mt. Edith Cavell, Jasper National Park, J.R.D., 1743; Maligne Canyon, Jasper National Park, J.R.D., 1748 (ALTA).

<u>BETULA</u> X <u>WINTERI</u> n. 'sp.' hyb.

<u>Betula</u> <u>resinifera</u> Britton x <u>B</u>. <u>papyrifera</u> Marsh.

<u>Arbor</u>, <u>plerumque</u> <u>20-30</u> <u>m</u>, <u>truncus</u> <u>usque</u> <u>ad</u> <u>5</u> <u>cm</u> <u>in</u> <u>diametro</u>. <u>Ramuli</u> <u>tenues</u>, <u>pubescentes</u> <u>vel</u> <u>glabri</u>, <u>glandifri</u> <u>vel</u> <u>non-glandifri</u>. <u>Cortex</u> <u>fuscus</u> <u>ad</u> <u>album</u>, <u>exfolians</u> <u>in</u> <u>schedis</u> <u>albis</u>. <u>Folia</u> <u>ovata</u>, <u>acuta</u> <u>ad</u> <u>subito</u> <u>acuminata</u> <u>habentia</u> <u>et</u> <u>fundum</u> <u>truncatum</u>, <u>cordatum</u>, <u>rotundatum</u> <u>vel</u> <u>cuneatum</u>, <u>et</u> <u>marginem</u> <u>crasse</u> <u>et</u> <u>ut</u> <u>solet</u> <u>inaequaliter</u> <u>di-serratum</u>, <u>5-7</u> <u>cm</u> <u>longa</u>, <u>3-4.5</u> <u>cm</u> <u>lata</u>, <u>et</u> <u>venas</u> <u>non-nunquam</u> <u>pubescentes</u> <u>in</u> <u>axillis</u> <u>infra</u> <u>et</u> <u>petiolos</u> <u>amplos</u> <u>circa</u> <u>20</u> <u>mm</u> <u>latos</u>. <u>Amenta</u> <u>pistillata</u> <u>in</u> <u>fructu</u> <u>glabro</u>, <u>pendulosum</u>, <u>3-4</u> <u>cm</u> <u>longa</u>, <u>8-10</u> <u>mm</u> <u>lata</u>; <u>habentia</u> <u>bracteas</u> <u>glabras</u>, <u>raro</u> <u>puberulentas</u> <u>cum</u> <u>lobis</u> <u>lateralibus</u> <u>late</u> <u>fatulis</u> <u>rotundatis</u>, <u>et</u> <u>lobo</u> <u>medio</u> <u>lanceolato</u> <u>acute</u> <u>usque</u> <u>ad</u> <u>rotunde</u>. <u>Samerae</u> <u>corpus</u> <u>1-2</u> <u>mm</u> <u>latum</u>, <u>2-4</u> <u>mm</u> <u>longum</u>, <u>ovatum</u>, <u>multo</u> <u>angustius</u> <u>quam</u> <u>eins</u> <u>ala</u>. <u>Numerus</u> <u>chromo-somorum</u> <u>2n</u> = <u>28 - 84</u>.

Tree, usually 20-30 m, trunk up to 5 dm in diameter, branches erect spreading and pendulous; branchlets slender, pubescent or glabrous, glandular or not glandular. Bark brown to white, exfoliating in thin sheets. Winter buds ovate, acute, dark chestnut-brown, glabrous and slightly resinous, 2-3 mm long. Leaves ovate, acute to abruptly acuminate, base truncate, cordate, rounded or cuneate, margin coarsely and mostly irregularly doubly-serrate, dull green above, lighter below, turning a light

clear yellow in autumn, 5-7 cm long, 3-4.5 cm wide, with a slender midrib, veins may or may not be pubescent in axils below; stomata averaging from 24-48 μ; petioles stout, about 20 mm long; stipules ovate, acute, ciliate, light green, caducous. Staminate catkins 1-3, clustered, sessile, 2-3 cm long in winter, becoming 6-8 cm long in spring, bracts ovate, acute to apiculate, puberulous, light brown to dark red-brown; pollen averaging from 24-26 μ in diameter. Pistillate catkins in flower cylindrical, slender, glandular, about 25 mm long on slender peduncles, in fruit glabrous, pendulous, 30-40 mm long, 8-10 mm wide; bracts glabrous, rarely puberulous, the lateral lobes wide-spreading, rounded, middle lobe lanceolate acute to rounded. Fruit a samara, body 1-2 mm wide, 2-4 mm long, ovate, much narrower than its wing. Chromosome number 2n = 28 - 84.

Types: Holotype: Emily Murphy Park, Edmonton, Alberta, Janet R. Dugle, 1814, June 17, 1962 (ALTA). (See Plate a15).

Distriubtion: Forested areas; Alberta, Saskatchewan, and Manitoba; northward to the tree line in the Northwest Territories, Yukon and Alaska; limited by the distribution of *Betula resinifera*.

Taxonomic Notes: This birch was named for Dr. John Mack Winter (1902-1964), student of the flora of the American midwest.

<u>Representative specimens</u>: ALBERTA: Botanic Gardens near Edmonton, J. R. D., 1368, 1369, 1371 (ALTA); North Saskatchewan River Bluffs near Edmonton, J. R. D., 1374, 1375, 1377, 1379, 1381, 1792, 1793, 1795, 1796, 1797, 2122, 2123, 2124 (ALTA); White Mud Creek bluff near Edmonton, J. R. D., 1387, 1388, 1390 (ALTA); Woods near Gunn on Lac Ste. Anne, J. R. D., 1392 (ALTA); Queen Elizabeth Park, Edmonton, J. R. D., 1584, 1585, 1586, 1587, 1589, 1590, 2070, 2072, 2074, 2075 (ALTA); Hill-top near Muir Lake, J. R. D., 1596, 1597, 1599 (ALTA); White Mud Creek Park, Edmonton, J. R. D., 1799, 2126, 2128 (ALTA); Bluff, University of Alberta, Edmonton, J. R. D., 1809, 1810, 1813 (ALTA); Emily Murphy Park, Edmonton, J. R. D., 1813, 1818, 1819, 1821, 1823 (ALTA); Camp Agape, Elk Island National Park, J. R. D., 2083, 2084, 2085, 2086, 2087, 2089 (ALTA); Hillside above bog near north entrance, Elk Island National Park, J. R. D., 2108 (ALTA); Meadow, Elk Island National Park, J. R. D., 2110, 2111, 2112 (ALTA); Roadside, Elk Island National Park, J. R. D., 2121 (ALTA); Ft. Fitzgerald, W. J. Cody and C. C. Loan, 3840 (MIN); 30 miles west of Whitecourt, E. H. Moss, 10664 (ALTA); 10 miles above Carcajou Settlement, H. M. Raup and E. C. Abbe, 4386 (MIN); Hill slope above river valley, Fort Saskatchewan, G. H. Turner, 2518 (DAO); Saskatoon Mt., east of Beaverlodge, L. Jenkins, 698 (DAO);

Watino, E. H. Moss, 7682 (DAO); Peace River, E. H. Moss, 7715 (DAO); East slope of Caribou Mountains, H. M. Raup, 2183 (US).

SASKATCHEWAN: 5 miles west of Wallwort, A. J. Breitung, 657 (DAO), 650 (MIN); Moose Mtn. Park, Kenosee Lake, H. A. Senn, 2526 (DAO); Gravelly beach, Moose Mtn. Park, Kenosee Lake, H. A. Senn, 2534 (DAO); Qu'Appelle valley, east of Craven, B. de Vries, 880 (DAO); Lake Athabaska, Wolverine Pt., H. M. Raup 6835 (ALTA)(GH); Vicinity of Warren Lake, 59°45'N., 102°50'W., G. W. Argus, 589-63 (SASK).

MANITOBA: West Hawk Lake, M. G. Dudley, July 9, 1939 (DAO).

NORTHWEST TERRITORIES: South of Fort Simpson on slope to River, W. J. Cody and J. M. Matte, 9258 (DAO); Fort Smith, W. J. Cody and C. C. Loan, 3796 (DAO); South shore of Kakisa Lake, J. W. Thieret and R. J. Reich, 4658 (DAO); Mile 19 along the Enterprise-Mackenzie River Highway, J. W. Thieret and R. J. Reich, 5603 (DAO); Kakisa Lake road about 3/4 mile from highway junction, J. W. Thieret and R. J. Reich, 4726 (DAO); Vicinity of eastern end of Brintnell Lake, H. M. Raup and J. H. Soper, 9589, 9578 (A).

<u>BETULA</u> X <u>SANDBERGII</u> Britton, Torrey Botanical Club Bulletin 31: 166 (1904)

<u>Betula</u> <u>pumila</u> var. <u>glandulifera</u> Regel x <u>B</u>. <u>papyrifera</u> Marsh.

<u>B</u>. <u>sandbergii</u> Britton, N. Am. Trees 256 (1908); Butler, Torrey Bot. Club Bull. 36: 430, Fig. 8 (1909).

<u>B</u>. x <u>sandbergii</u> Britton in Rosendahl, Rhodora 30: 125-129 (1928); Minn. Bot. Stud. 4: 442-459 (1916); Sargent, Man. of the Trees of N. Am., Vol. I: 213 (1922), reprinted 1962.

Large shrub, 3-6 m tall, usually several trunks present, up to 2 dm in diameter, branches ascending and spreading; branchlets somewhat glandular, pubescent, green becoming brown. Bark non-exfoliating, brown to light and exfoliating. Leaves ovate to elliptic, mostly acute at the apex, rounded to cuneate at the base, margin serrate; dark green on the top, light green beneath, turning yellow in autumn, very glandular and slightly pubescent below, 3-5 cm long, 2-4 cm wide; stomata averaging 31-36 μ; petioles 1-1.5 cm long, glabrous. Staminate catkins 1-3, clustered, 1-2 cm long during the winter elongating to 6 cm long or longer in the spring; pollen averaging from 24-26 μ in diameter. Pistillate catkins about 15 mm long in flower, in fruit cylindric, 2-2.5 cm long, about 6 mm wide, erect or pendulous on slender peduncles; their bracts pubescent,

lobes ascending, middle lobe acute, rather longer than the truncate lateral lobes. Fruit a samara, body 1-2 mm long, 0.5 - 1.5 mm wide, ovate to obovate, narrower than its wings. Chromosome number 2n = 56 - 84.

Type: Holotype: Swamps, Hennepin County, Minnesota, June, 1890, J. H. Sandberg (NY). (See Plate a16).

Distribution: Common where the parental species occur together; central Alberta and Saskatchewan; south to Minnesota; and west to North Dakota.

Representative specimens: ALBERTA: Devon Road, Clymont, Alberta, J. R. D., 1778 (ALTA); White Mud Park, Edmonton, J. R. D., 1800, 1801, 1802, 1803, 1804, 1807, 2129, 2131, 2148, 2151, 2152, 2199, 2200, 2201 (ALTA). SASKATCHEWAN: Wolverine Pt., Lake Athabaska, H. M. Raup, 6834 (GH); 11 miles southwest of Wallwort, A. J. Breitung, 391 (DAO); South shore of Lake Athabaska, east of William River, G. W. Argus, 261-62, 266-62, 263-62, 264-62 (SASK). MANITOBA: 3 miles north of Cypress River, H. H. Marshall, 2 (DAO).

MINNESOTA: Shore of Moore Lake, Anoka Co., C. O. Rosendahl and A. M. Johnson, Sept., 1917 (MIN); Purgatory spring, Minnetonka, C. O. Rosendahl, 2502 (MIN); ½ mile south of Cold Springs, J. W. Moore and N.L. Huff, 18399 (MIN); Star Island, Cass Lake, Cass Co., J. B. Moyle and E. L. Nielsen, 1775 (MIN); East shore of West Lost Lake, 7.2

miles north of Underwood, Ottertail Co., J. W. Moore and D. L. Jacobs, 14765 (MIN); Decodon Pond, Anoka Co., M. F. Buell, 1808a (MIN); North of Lake Vadnais, C.O. Rosendahl, P.A. Rydberg, 5176 (MIN); Duluth, Olga Lakela, 1576 (MIN); North Park Boundary Road, Clearwater Co., L. R. Sevigny, July 14, 1954 (MIN); Floating Bog Bay, Itasca Park, Clearwater Co., M. F. Buell, 2040 (MIN); Floating Bog bay, C.O. Rosendahl, 5262 (MIN); Buffalo State Park, Clay Co., O.A. Stevens, 1035, 1036 (MIN); North boundary Itasca Park, Clearwater Co., M. F. Buell, 485 (MIN); Cultivated on University of Minnesota campus, Aug. 8, 1928 (MIN); Edge of swamp, Floating Bog Bay, Itasca State Park, E. L. Nielsen, 1891 (MIN); Turtle Lake ¼ mile west of Lexington Ave., Ramsey Co., J. W. Moore and C. O. Rosendahl, 21356 (MIN).

NORTH DAKOTA: Anselm, 5 miles east and 1 mile south, Ransom Co., O. A. Stevens, 1307 (DAO); Barrie, Richland Co., O. A. Stevens, 1306 (DAO); Anselm, Ransom Co., O. A. Stevens, 1308 (DAO).

Geographical Distribution Related to the Pleistocene

Ice covered much of northern North America during the glacial advances of the Pleistocene epoch. Plant survival has, however, been suggested as probable in several areas. Refugia have been postulated for the Yukon Valley of Alaska, the southern Rocky Mountains, the "driftless" area south of the Great Lakes, the Alaskan coast, the Arctic Archipelago and its continental shelves, the Gaspé Peninsula and other areas around the Gulf of St. Lawrence, and the Queen Charlotte Islands (Fernald, 1925; Hultén, 1937). Fernald's proposal of refugia in the Gaspé Peninsula and Labrador has been widely discussed and a number of workers strongly oppose Fernald's opinion (Deevey, 1949). However, a recent paper (Ives, 1963) suggests that several areas in Labrador as well as the Shickshock Mountains in the Gaspé Peninsula actually were unglaciated in the maximum Wisconsin advance and could have been refugia.

When the ice receded, the area that had been ice-covered was open for colonization. The present distribution patterns may give some indication of the areas from which the plants have migrated in post-glacial times. The patterns of post-glacial migration may help to explain the occurrence and distribution of hybrids.

Hultén (1937) has suggested that Betula resinifera radiated from the Yukon valley. This birch is found mostly in glaciated areas and not in montane areas. It does not reach Hudson's Bay. Raup (1947) has suggested it is a continental western American radiant, although it seems more likely it is a radiant from the Yukon valley since its present distribution indicates it has not been in the mountains.

Hultén (1937) and Raup (1947) have also suggested that Betula glandulosa and B. papyrifera are continental western American radiants and survived the ice in the upper Yukon valley, south of the border of the ice in the Rocky Mountains, at the Great Lakes, and on the continental shelf of eastern America and on refugia around the Gulf of St. Lawrence. B. glandulosa probably also survived the glaciation in Greenland. These birches are not coast-bound in western America and do not reach further west than the Yukon valley. From the refugia they spread in post-Valderan time and filled the areas which had been covered by ice.

Raup (1947) suggested and the author agrees that B. fontinalis is an arctic montane radiant, surviving the Pleistocene in the Yukon valley and in the Rocky Mountains. It is at present a forest species. Following the retreat of the ice, B. fontinalis radiated from these two centers and possibly met in the Canadian Rocky Mountains. It is

suggested that _B. pumila_ var. _glandulifera_ survived the glaciation south of the ice sheet and has gradually spread northward following the retreat of the ice.

A possible explanation for the distribution of hybrids involving the above taxa may be advanced, taking into account the migration following the Valderan glaciation. _Betula resinifera_ migrated south and east, finally coming into contact with the _B. papyrifera_ elements which survived south of the ice and in the Great Lakes refugia, and migrated north. Swarms of _B. x winteri_ were thus formed. Probably the _B. papyrifera_ elements which survived the glaciation in the Rocky Mountain refugia were not involved in these hybrid populations. However, it is possible that the _B. papyrifera_ which survived in the Yukon valley is hybridizing with _B. resinifera_ from the same place.

In its southern and eastern migration, _Betula resinifera_ also came in contact with _B. pumila_ var. _glandulifera_ which was migrating north and west from refugia south of the ice. In scattered areas swarms of _B. x uliginosa_ have been thus formed.

Betula glandulosa originating in the upper Yukon valley and south of the ice in the Rocky Mountains radiated south and east from the Yukon valley refugium and north in the mountains, and came in contact with _B. pumila_ var.

glandulifera which was radiating north and west from areas south of the furthest extension of ice. These hypotheses are based only on the behavior of the western species. Many hybrid populations of *B.* x *sargentii* are thus found in the areas near the Rocky Mountains, and in Northwest Territories and Yukon Territory. This widespread hybrid, *B.* x *sargentii* found in the areas near the Rocky Mountains, thus came into contact with *B. papyrifera* which migrated north from refugia in the southern Rocky Mountains and perhaps *B. papyrifera* which migrated south from refugia in the upper Yukon valley, and hybridized to form *B.* x *arbuscula*.

Betula fontinalis and *B. papyrifera* have similar origins in refugia in the upper Yukon valley and south of the ice in the Rocky Mountains. *B. papyrifera* which migrated from south of the ice in other areas of North America also may be involved. These two species are in contact in the southern Rocky Mountains, and all the way north along the mountains up to the Yukon territory. Thus, another widespread hybrid, *B.* x *utahensis* is found in all of these areas as well as east of the Rockies where *B. fontinalis* comes in contact with populations of *B. papyrifera* which probably have a more southeastern origin.

Betula glandulosa and *B. fontinalis* with origins in two areas, the upper Yukon valley and south of the

Pleistocene ice in the Rocky Mountains migrated south and east from the Yukon origin and north from the Rocky Mountain origin. These species came in contact in the Canadian Rocky Mountains and in Yukon Territory where a very common hybrid, B. x eastwoodae is found. B. glandulosa from refugia south of the ice also migrated northward following ice retreat and came in contact with the eastward migrating B. fontinalis from the upper Yukon valley refugium producing hybrid populations in the Northwest Territories.

It has been suggested by Hagerup (1932) that polyploids are more tolerant of extreme ecological conditions than their diploid relatives. Many exceptions to this hypothesis have been found (Clausen, Keck, and Hiesey, 1945; Gustafsson, 1948) and some additional exceptions are shown here, in which Betula glandulosa, B. resinifera, and B. fontinalis (all with 2n = 28) are most commonly found in more northern regions than are B. papyrifera and B. pumila var. glandulifera (2n = 56, 70, 84). The distribution of western Canadian birches may eventually provide evidence for the theory of Stebbins (1950) that polyploids were the most active early colonizers of the bare ground left after the retreat of the ice.

INTRODUCTION TO BIOSYSTEMATIC TREATMENT OF BETULA IN WESTERN CANADA

Techniques Used in Hybrid Analysis

In undertaking this investigation, collections of birches were made in geographically distinct and ecologically varying areas in western Canada, mainly Alberta and British Columbia, during 1961, 1962, and 1963. Specimens collected from each sample included several branches with a number of mature leaves, twigs of the current year's growth and the previous year's growth, and if possible, staminate and pistillate catkins. The color of the bark was recorded or a specimen was collected.

In population analysis one endeavors to compare consistent and equivalent characters and stages of development. Therefore, in obtaining measurements from leaves and catkins, the ten largest were chosen in order to obtain maximum values rather than a mean value because the developmental aspects are thus discounted and errors in selecting an average are minimized. Tracings of leaves and drawings of fruits and bracts were made showing the variation present in the populations. Three main techniques for the presentation of data were used: polygonal graphs, hybrid index, and pictorial scatter diagrams.

a. Polygonal graphs

In recent years the polygonal graph method applied by Davidson (1947) to population analysis has been used extensively

(Froiland, 1952; Haskell, 1960; Clausen, 1962). The graph consists of a circle with as many radii as there are characters selected for comparison. The characters which are measured along each radius are assigned absolute, relative, or arbitrary values. The character values exhibited by each sample are plotted individually along each radius, and the points are joined. Thus each specimen is represented by a polygon, and the population is represented by a series of polygons. The advantage of polygonal graphing is that members of a population may be compared with respect to a number of varying characters at a glance. (See Figure a20).

b. Hybrid index

Another method of analysis used in the study was the hybrid index method, described by Anderson (1949). In this technique a character is selected which is varying in the population. A number 0 is given to the condition typical of one extreme in the character and from 1-4, depending on the character, is given to the other. For example, using the character leaf pubescence, one extreme is completely glabrous, the other is pubescent, and a third possibility is intermediate in pubescence. In this case the numbers would be assigned: Glabrous leaves - 0, intermediate leaves - 1, and pubescent leaves - 2. When the index numbers for each of the characters have been determined for each sample studied, the numbers are totaled. This total is the "hybrid index value" of the sample. A bar graph is constructed on which the hybrid index values are plotted against their fre-

quency within the population. Thus the probable presence or absence and amount of hybridization between the parental forms can be determined readily by an examination of the graph. (See Figure 9).

c. Pictorialized scatter diagrams

Pictorialized scatter diagrams (Anderson, 1949) were prepared as an additional method for showing character association. Two characters used in the hybrid index serve as coordinates, and each individual in the population is plotted on these axes. Additional characters are depicted by variation in the symbols, for example, the glabrous condition of leaves may be plotted as a black spot (●), the intermediate condition as a black and white spot (◒), and the pubescent condition as a white spot (O). Other characters may be illustrated by appendages to the spots. Thus an overall picture of the population variation can be seen. (See Figure 10).

Other characters measured and statistical analyses

A number of the above characters and others not discussed above were measured and some subjected to analysis of variance. Among these were pollen fertility, pollen size, number of pores per pollen grain, and size of stomata.

Pollen fertility was estimated by stainability with cotton blue in lactophenol. The diameter of the pollen grain (at its widest place) was determined using a micrometer eyepiece.

The stomatal length was determined on epidermal prints

obtained using the technique described by Celarier and Mehra (1958). Collodion was substituted for the cellulose nitrate - acetone mixture. The length of stomata was measured with an eyepiece micrometer. A comparison of stomatal length measured with collodion and length measured with epidermal peels was made, and it was found that measurements were 21-29 per cent higher using epidermal peels. Therefore, in descriptions, the measurements using epidermal peels which are the true measurements are used. If comparisons with epidermal peel measurements are made using these data from collodion prints, the measurements can be increased by approximately 25 per cent.

The analyses of variance were carried out using several of the above measurements and tests of significance were made at the 5 per cent and 1 per cent levels. Duncan's multiple range test (1955) was applied.

Chromatography

In a series of papers Clausen (1962, 1963) has described a chromatographic technique for the comparative analysis of birch taxa using extracts from the inner bark. His results were of sufficient interest to warrant an investigation of their value in the present study. Samples of inner bark were collected and ethanol extracts made (5 gms/50 ml) using the technique of Clausen (1963, letter). The extracts were concentrated to 1/10 original volume.

Aliquots of the concentrated extracts were spotted on Whatman No. 1 filter paper and placed in a chromatographing cabinet previously equilibrated with ammonium hydroxide, secondary butyl alcohol, and water. The chromatograms were developed by descending irrigation for 24 hours, using secondary butyl alcohol equilibrated with water as the irrigating solvent. The air-dried chromatograms were sprayed with a 2 per cent aqueous solution of sodium carbonate and again dried. The treatment with sodium carbonate caused fluorescent spots to appear on the chromatograms when these were viewed under ultraviolet light. Some chromatograms were sprayed with benzidine spray to test for the presence of sugars, while others were sprayed with ninhydrin to test for amino acids.

Chromatograms of leaves were also prepared following the technique of Alston and Turner (1962). An equal number of leaf discs for each individual was prepared and extracted in darkness for 24 hours in 10 ml of 99:1 solution of methanol : concentrated HCl. The extract was concentrated to 2 ml and aliquots of the extract were spotted on Whatman No. 1 filter paper and placed in a chromatographing cabinet. The chromatograms were developed by descending irrigation for 24 hours, using 3:1:1 solution of tertiary butyl alcohol : glacial acetic acid : water, as the irrigating solvent. In some cases the single direction air-dried chromatograms were studied. In others, the air-dried chromatograms were run in another direction using 85:15 glacial acetic acid : water for four hours. The chromatograms were again air-dried. These were then studied

under ultraviolet light, in ammonia vapor in daylight, and in ammonia vapor in ultraviolet light.

Duplicate series were run at a later date to determine predictability and reproducibility. It was found that this technique was of use as an additional character, but that chromatograms, as with any morphological characters, must not be overemphasized. One of the major difficulties is the difference in qualitative color determination.

Cytology

Mitotic chromosome preparations were obtained from root tips of germinating seed or potted birches which were fixed in freshly mixed acetic-alcohol (1:3), Carnoy, or Newcomer (1953) fixatives following pretreatment with 0.002 M 8 hydroxyquinoline or a saturated paradichlorobenzene solution. Squashes were made in acetic orcein, acetocarmine, propionocarmine, and Feulgen stain. Some root tips were prepared with paraffin sectioning and stained in crystal violet. In obtaining root tips for the cytological studies, seeds were germinated on moist filter paper at room temperature and the seedlings were transferred to pots which were grown in temperate green house.

Staminate catkins collected in the last week of July and the first week of August were fixed as above and sectioned from paraffin and stained in crystal violet. Squashes of this material were unsuccessful because meiotic stages suitable for chromosome counting are very rapid as judged by the number of mother cells in these stages, and it proceeds in only a few

anthers at a time. In order to insure obtaining meiosis, longitudinal sections of the staminate catkins were mounted in series. Photomicrographs were taken with a Zeiss photomicroscope using KB14 film.

The birches have chromosomes approximately 1 μ or less in length. Accurate counts are reasonably easy to obtain on the 28 and 56 chromosome birches, but the higher numbers are much more difficult. Johnsson (1949) has stated, "On account of the high chromosome numbers and of the frequently poor quality of the prepared specimens, the counts are subject to a certain degree of uncertainty, which amounts to at least $\pm$ 2 chromosomes but in no circumstances exceeds $\pm$ 5 chromosomes."

Meiotic irregularities such as lagging chromosomes and "sticky" chromosomes were found to be fairly common. Some examples are shown in Plate a17, Figures 1-4. Two irregularities described by Woodworth (1931), cytomixis (in which cytoplasmic bridges form between pollen mother cells) and chromatolysis (in which bands of chromosome material connect pollen mother cells) were not noted.

Introgressive Hybridization

A number of the techniques listed above were designed for analysis of introgressive hybridization, which was found to be an important feature of this study.

Introgression is the gradual diffusion of genes from one population into another. However, the original hybridization is not introgression which is the result of backcrossing

and the introduction of genes into one or the other, or in some cases both, of the parental populations. In a population suspected of being subjected to introgression, Anderson (1949, 1951, 1953) has suggested several ways of testing: 1) the presence of discordance in the apparent parental forms; 2) being able to predict one parent by an examination of the variation in the other and in the hybrids; 3) all the variation in one parent is in the direction of the other; 4) for unidirectional gene flow a gap between one parent and the hybrids, and no apparent gap between the hybrids and the other parent; 5) for unidirectional introgression, the hybrids are closer to one parent than to the other. Most commonly there is a disturbance of the habitat or intermediate habitats present for the hybrids (Anderson, 1948).

Anderson (1953) has also described a number of tests by which the distinction can be made between introgression and the gene pool hypothesis. In the gene pool hypothesis the intermediate forms are ancestral and provide the basis for the development of additional species. The five tests which Anderson proposed are: 1) the loose association of variable characteristics of the variation pattern in artificially produced hybrids and backcrosses; 2) the introgressants found in floristically newer or disturbed areas; 3) sterility, if present, showing up in the intermediates; 4) ability to predict the introgressing species by the method of extrapolated correlates; and 5) the similarity of experimental hybrids and backcrosses with the

supposed hybrids found in the field.

In the analyses beginning on page 130 several of the above methods and techniques have been used, although not all of them were used for each population.

BETULA PUMILA VAR. *GLANDULIFERA* X *BETULA RESINIFERA* (*B*. x *uliginosa*)

The area referred to here as "Ponoka Bog" is located on Highway 2, 71 miles south of Edmonton, Alberta. A preliminary examination of the area established the fact that *Betula resinifera* was present, along with typical individuals of *B*. *pumila* var. *glandulifera* (see Figure 7 and Plate 8, Figs. 1-4).

Although it was easy to distinguish some individuals which clearly belonged to one or the other of the species named above, others were so variable as to make it impossible to assign them with any certainty to either of the above taxa on the basis of characters normally used in identification. Wide variations of the two species and many intermediate forms were noted throughout the population. This widespread blending and recombination of species characters among the birches in the Ponoka bog strongly suggested that natural hybridization might be the cause of the variation pattern. A detailed study was undertaken to see if this was the case. The entire stand of trees and shrubs was analyzed as if it were a single heterogeneous population. The population of birches studied consisted of 99 individuals, randomly collected, and of these 63 bore pistillate catkins and are represented in the analysis.

FIGURE 7.

Map of Ponoka bog showing distribution of _Betula resinifera_, _B_. _pumila_ var. _glandulifera_ and hybrids. The approximate altitude above sea level of the path in the lower right corner is 2730'.

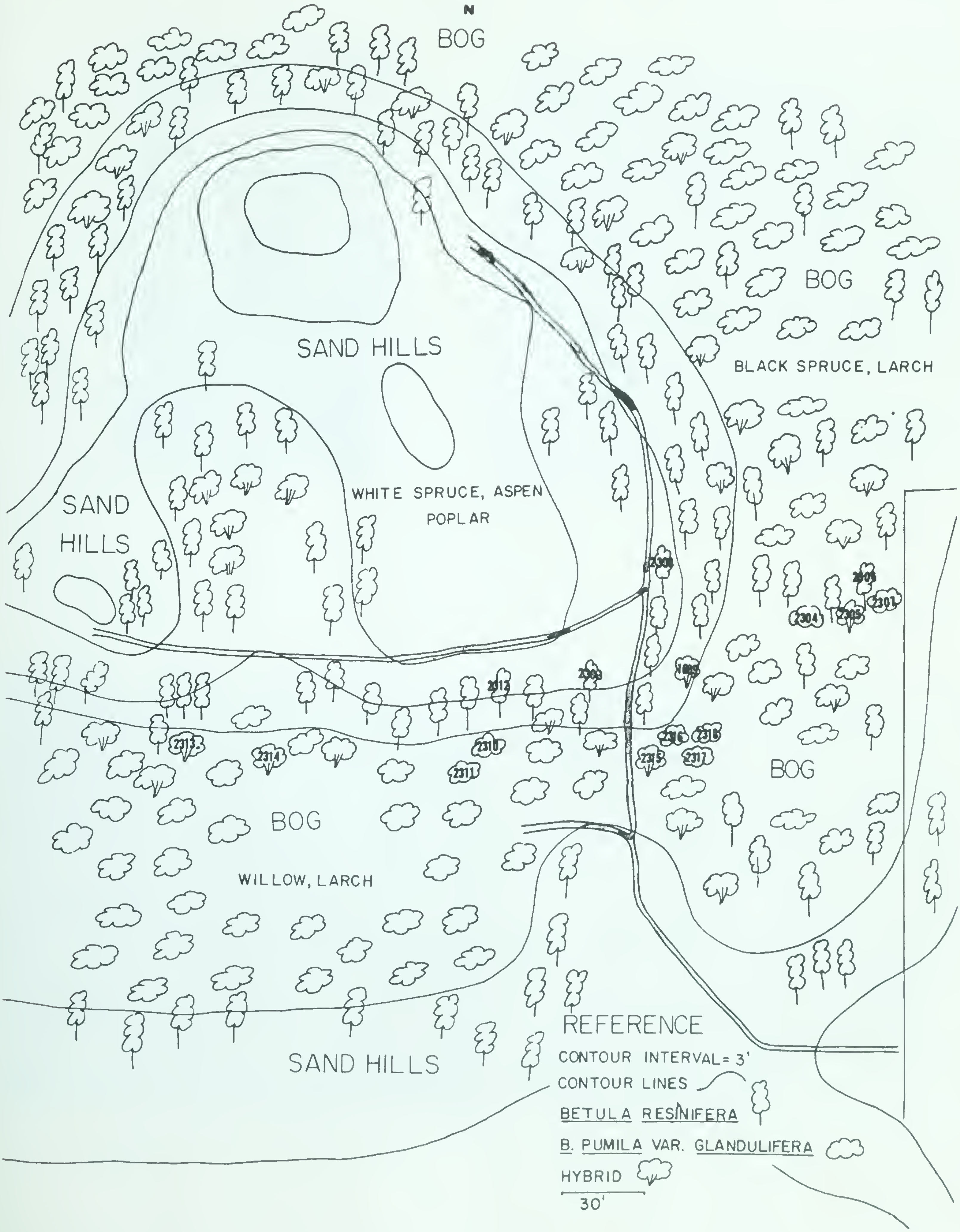

N
BOG
SAND HILLS
BOG
BLACK SPRUCE, LARCH
SAND
HILLS
WHITE SPRUCE, ASPEN
POPLAR
2308
2304
2305
2312
2313
2314
2310
2311
2316
2318
2315
2317
BOG
BOG
WILLOW, LARCH
SAND HILLS
REFERENCE
CONTOUR INTERVAL = 3'
CONTOUR LINES
BETULA RESINIFERA
B. PUMILA VAR. GLANDULIFERA
HYBRID
30'

PLATE 8.

Photographs of Ponoka bog birches.

Fig. 1. *Betula resinifera* (2308)

Fig. 2. *Betula pumila* var. *glandulifera* (2310), left; *B. resinifera* (2312), right.

Fig. 3. *Betula* x *uliginosa* (2315)

Fig. 4. *Betula* x *uliginosa* (1689), type shrub.

1.

2.

3.

4.

Characters of Gross Morphology Used in the Analysis

A summary of the morphological characters used in the analysis is in Table 3.

TABLE 3.

Gross morphological characters of *Betula resinifera* and *B. pumila* var. *glandulifera* used in the analysis.

B. pumila var. *glandulifera*	*B. resinifera*
Bark brown	Bark pale rose-brown to white
Bark non-exfoliating	Bark exfoliating
Leaves 2-3 cm long	Leaves 4-7.5 cm long
Leaves 1-3 cm wide	Leaves 3-6 cm wide
Leaves obovate	Leaves trullate to broadly ovate
Leaves obtuse to acute at apex	Leaves acuminate at the apex
Leaves cuneate to round - cuneate at the base	Leaves truncate to rounded at the base
Leaf margin crenate	Leaf margin doubly-serrate
Less than 14 crenations on one leaf margin	More than 24 crenations on one leaf margin
3-5 pairs of lateral leaf veins	6-7 pairs of lateral leaf veins
Fruiting catkins 1-2 cm long	Fruiting catkins greater than 2.5 cm long
Fruiting catkin 6-8 mm wide	Fruiting catkin 9-11 mm wide
Wings of samara much narrower than body	Wings of samara much broader than body

Various intermediate characters were recognized and these various categories can be seen in Table al and the key

to Figure a20.

It was found that base of the leaves, even though it has been used as a distinguishing character in the past, was the least useful character, since both parental species had a complete range of variation (truncate, round-truncate, round-cuneate, and cuneate). Variation in the leaves of this population is illustrated in Figure a18.

Although bracts have been used in the past as differentiating characters (Butler, 1909), they were not used in the analysis because so much variability was found, even within the same catkin. Variation in bracts and samaras within the population is shown in Figure a19.

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the characters on each of the twelve radii of the graphs are shown in Figure a20. A selected group of representative polygons is shown in Figure a21.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are indicated in Table a1. For each character, the index value of 0 is typical of one extreme in the character, and the index value of 3 is typical of the other extreme. Variation from these extremes is indicated by the intermediate values. A typical *B. pumila* var. *glandulifera* index ranges from 0-4 while a *B. resinifera* index

ranges from 19 - 24. These ranges were arbitrarily selected.

The total index value for each tree was determined, and a bar graph was constructed upon which the hybrid index values were plotted against their frequencies (Figure 9). It can be seen that three peaks are present, one within the *Betula pumila* var. *glandulifera* range, one within the *B. resinifera* range, and a group of intermediate individuals which have hybrid index values from 5-12.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of five leaves and the number of pairs of leaf veins. Each individual was plotted (See Figure 10).

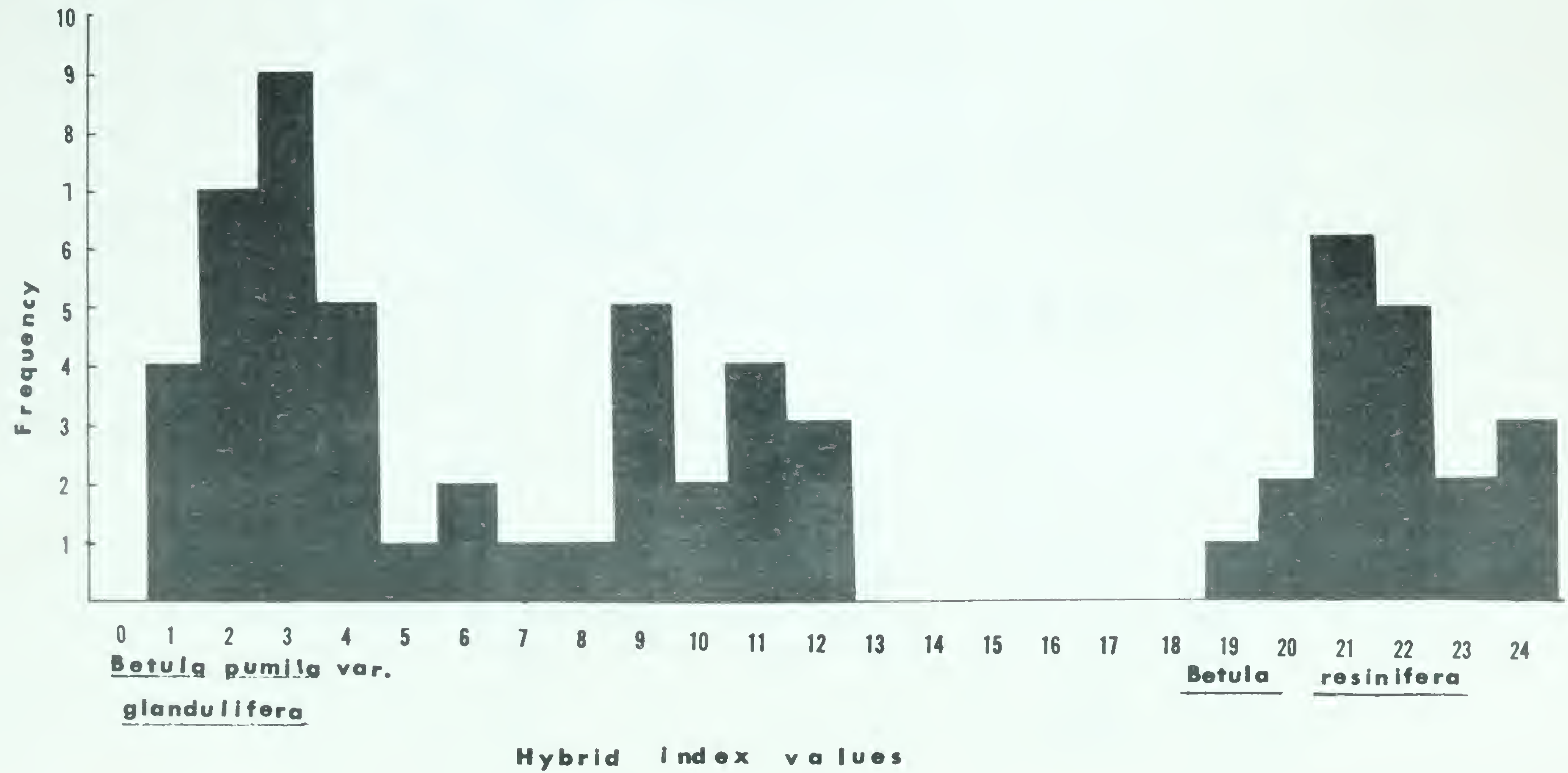
Correlation Coefficients

Coefficients of correlation were determined in six of the characters of Ponoka birches listed in Table 3. Each of these characters (number of teeth, pairs of veins, pistillate catkin length, pistillate catkin width, leaf length, and leaf width) was correlated with each of the other five. The results are shown in Table 4. Several of the pairs of characters show a high degree of correlation, which is not surprising since four of them are leaf characters.

A negative correlation is found between pistillate catkin width and pairs of lateral veins (at 5% level) and also between pistillate catkin length and width of leaf (at 1% level).

FIGURE 9.

Frequency of hybrid index values of <u>Betula</u> <u>pumila</u> var. <u>glandulifera</u>, <u>B</u>. <u>resinifera</u>, and hybrids.



Frequency
10
9
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Betula pumila var. glandulifera
Betula resinifera
Hybrid index values

FIGURE 10.

Pictorial scatter diagram of Ponoka bog birches

Key

Bark

Beige or pink-white exfoliating

Rose-gray and brown exfoliating

Brown and exfoliating

Brown and non-exfoliating

Leaf margin

Crenate

Crenate-serrate

Serrate

Doubly-serrate

Leaf shape

Widest above the mid-line

Widest above and at the mid-line

Widest at the mid-line

Widest below the mid-line

Leaf tip

Round

Round-acute

Acute

Acuminate

Samara wing

Much narrower than body

Narrower than body

As broad as body

Broader than body

Note: When necessary to avoid overlapping, appendages are bent.

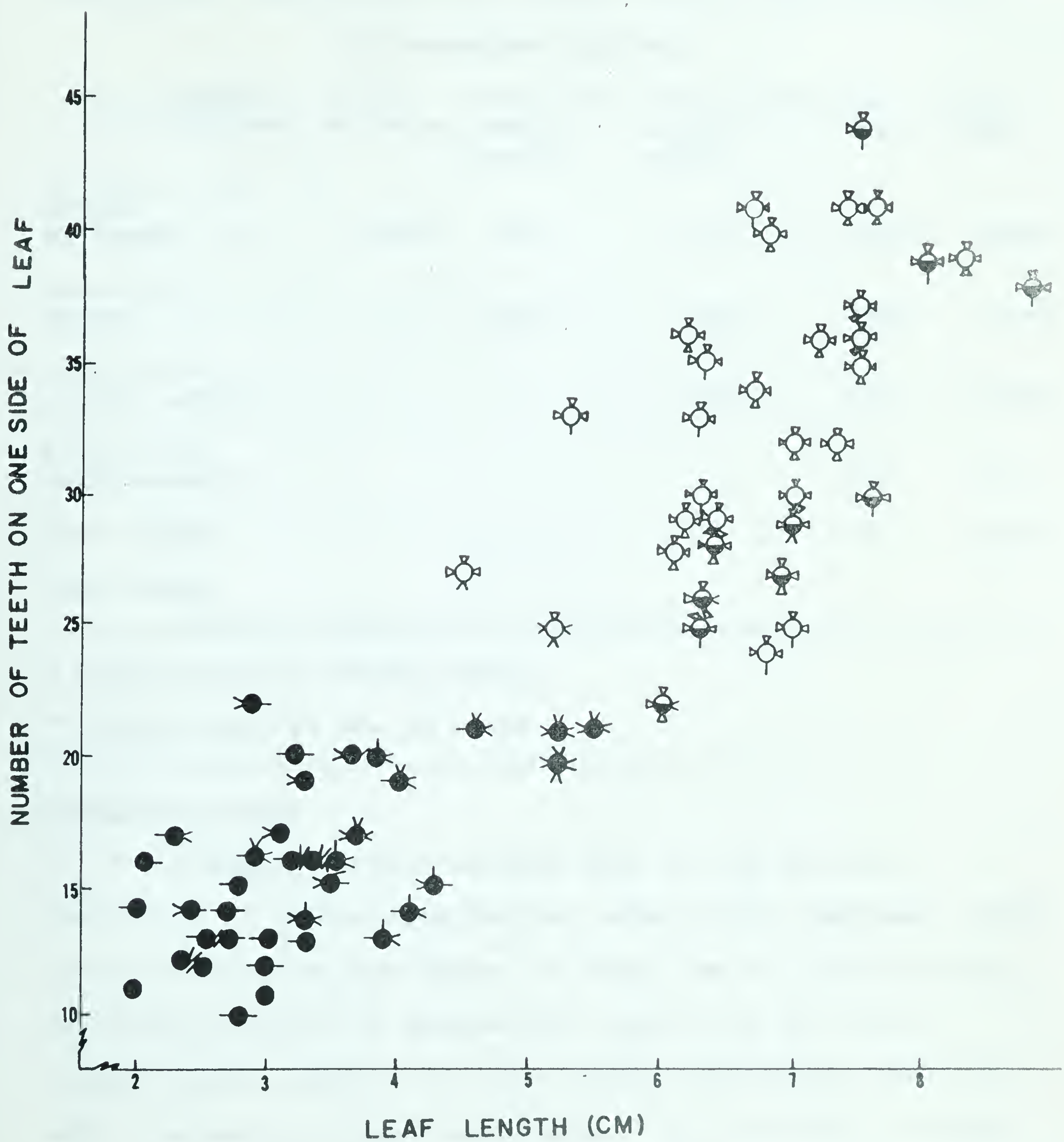

NUMBER OF TEETH ON ONE SIDE OF LEAF
LEAF LENGTH (CM)
10
15
20
25
30
35
40
45
2
3
4
5
6
7
8

TABLE 4.

Correlation coefficients of 6 hybrid index characteristics in Ponoka bog birches.

	Number of teeth	Pairs of veins	Pistillate catkin length	Pistillate catkin width	Leaf length	Leaf width
Number of teeth	-	.721**	.289	.009	.874**	.628**
Pairs of veins		-	.288	-.509*	.782**	.539**
Pistillate catkin length			-	.008	.166	-.608**
Pistillate catkin width				-	.015	.028
Leaf length					-	.828**
Leaf width						-

* significant at the 5% level

** significant at the 1% level

Germination Data

In *Betula*, fruits develop even if the seed has aborted or if pollination has not taken place (Johnsson, 1941) and therefore the germination is often low if the fruits are not examined prior to germination tests, and the fruits without seeds removed. In none of the germination tests was such a screening process undertaken. In the Ponoka birches, there is some evidence of reduction of fertility in the hybrids. The data are in Table 5.

TABLE 5.

Percentage germination of the fruits of Ponoka bog birches

Taxon	Hybrid indices	Number of individuals	Number of seeds planted	Percentage germination
_B_. _pumila_ var. _glandulifera_	0 - 4	8	292	9.9%
_B_. _resinifera_	19 - 24	5	270	4.4%
_B_. x _uliginosa_	5 - 18	9	747	1.2%

Stomata and Pollen Grain Morphology

The distribution of mean stomatal lengths of these taxa is presented in Table a2. A summary of stomatal size data is in Table 6.

TABLE 6.

Size of stomata (μ) in Ponoka bog birches.

Taxon	N	Range	mean	S.D.
_B_. _pumila_ var. _glandulifera_	14	22.0-32.5	28.8	2.84
_B_. x _uliginosa_	22	17.3-29.8	24.7	4.37
_B_. _resinifera_	18	16.5-24.4	20.7	2.19

A greater variation was thus found in hybrid stomatal length. The analysis of variance (Table 7) demonstrated that the difference among the means of the three taxa was highly significant. Duncan's multiple range test revealed that the mean of var. _glandulifera_ was significantly different from the mean of the hybrid and that those two taxa were significantly different from _B_. _resinifera_.

TABLE 7.

Analysis of variance in stomatal length in Ponoka bog birches.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	375.032	2	187.516	16.398**
Within taxa	594.618	52	11.435	
Total	969.650	54		

** significant at the 1% level

The distribution of mean pollen diameters of the three taxa is presented in Table a3. A summary of pollen size data is in Table 8.

TABLE 8.

Pollen size (μ) in Ponoka bog birches.

Taxon	N	Range	Mean	S.D.
B. pumila var. glandulifera	8	20.5-25.2	22.8	1.89
B. x uliginosa	13	17.7-26.6	22.1	2.28
B. resinifera	13	17.2-24.2	20.9	2.47

As can be seen, the variation was approximately equal in all three taxa and no more than a tendency for var. glandulifera to have larger pollen than B. resinifera can be inferred. The analysis of variance (Table 9) demonstrated that the difference among the means of the three taxa was not significant. Since there is not significant F, the application of Duncan's test is not necessarily warranted. However,

when applied, it was found that no mean was significantly different from any other.

TABLE 9.

Analysis of variance in pollen diameter in Ponoka bog birches.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	20.851	2	10.425	2.013
Within taxa	160.518	31	5.178	
Total	181.369	33		

It was found that grains having more than the usual three pores were fairly common in the hybrid pollen. Löken (1957) has noted that this occurs in about 2 per cent of the pollen in Betula verrucosa in adverse conditions in Norway, and Clausen (1962) has reported the same situation in B. x sandbergii in Minnesota. In B. x uliginosa (see Plate 11) it was found that 4.8 per cent of the pollen grains have more than three pores. This contrasts with the two parents in which 0.4 per cent of the pollen grains have more than three pores. A condition not commented upon by either Clausen or Loken is that in which pollen grains from a single anther may have both more and less than three pores. In the hybrids 15.2 per cent of the grains do not have three pores while in the two parents only 2 per cent do not have three pores.

The pollen was checked for stainability, and it was found that Betula resinifera pollen was 97 per cent stainable

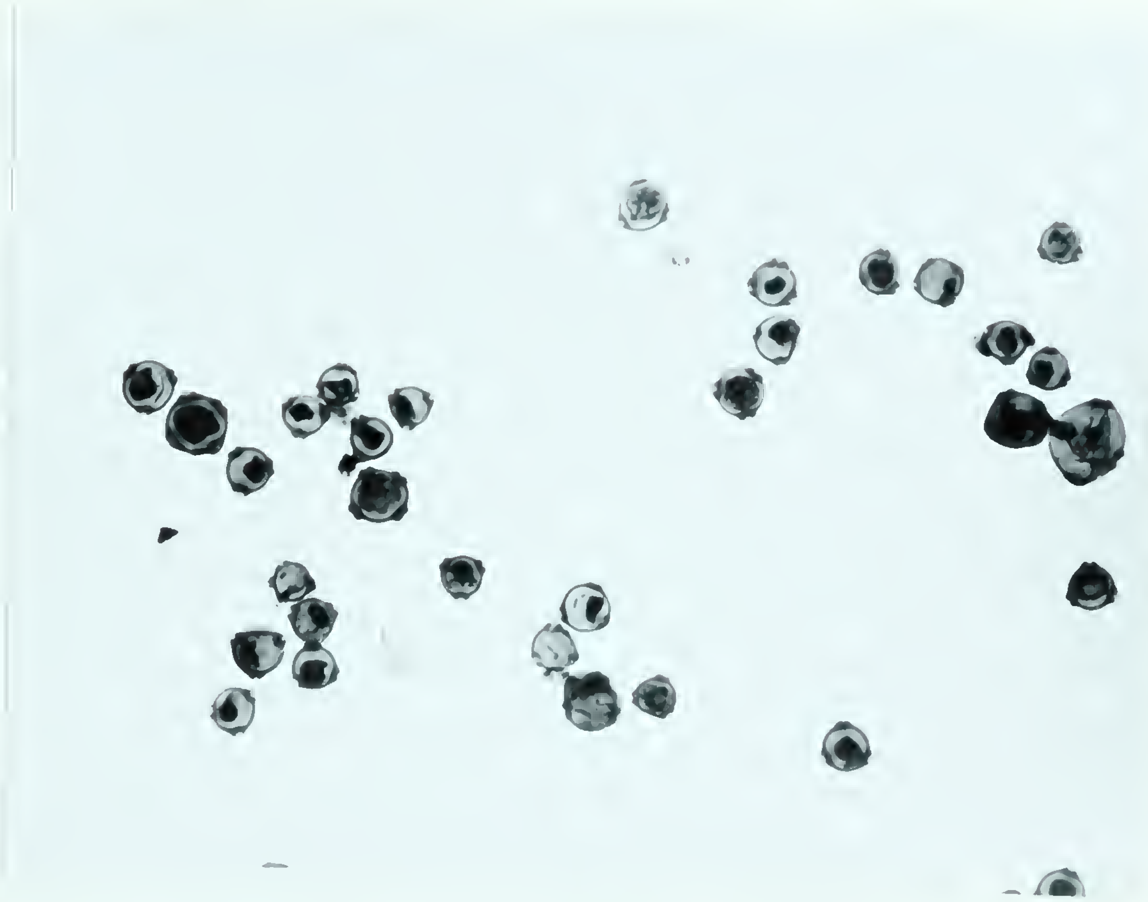


PLATE 11

Pollen of Betula x uliginosa, 1704 (x 250).

Note the variation in size and the fact that several of the pollen grains have more than three pores.

in cotton blue - lactophenol, B. pumila var. glandulifera pollen was 93 per cent stainable, and hybrid birch pollen was 79 per cent stainable.

Chromatography

Figure 12 presents tracings of chromatograms of Ponoka bog birches. The first eight chromatograms (2307a, 2310, 2307, 2311, 2316, 2317, 2304, and 2318) are made from extracts of Betula pumila var. glandulifera bark. The next five chromatograms (2315, 2314, 2313, 2305 and 1689) are extracts from B. x uliginosa bark. The last four (2306, 2312, 2308, and 2309) are extracts from B. resinifera bark. These are arranged in order of hybrid index. The spots were invisible in daylight except that the two spots nearest the solvent front were yellowish in appearance. The color of spots discussed in the following refers to their fluorescence under ultraviolet light. Clausen (1963) found that B. pumila var. glandulifera typically had three purple spots of about equal size at Rf's of 0.16, 0.22, and 0.29. Clausen's technique was followed as closely as possible, but varied in date of collection and temperature of storing. There were no spots visible under ultraviolet light at lower Rf's than 0.42 while none of the spots which Clausen used in his analysis were higher than Rf 0.30. However, Alston and Turner (1963) have said that comparisons based on Rf's should not be made. There was no "typical" chromatogram for B. pumila var. glandulifera, and the number of spots varied from

FIGURE 12.

Chromatograms of the inner bark of Ponoka bog birches arranged in order of hybrid index.

Each is marked with a collection number.

<u>Key</u>

Bright blue

Light blue

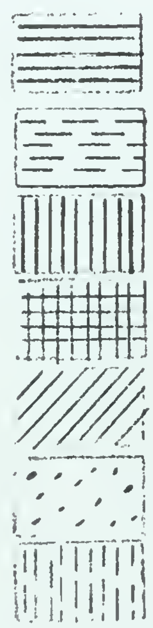
Bright purple

Dark purple

Green and blue-green

Yellow and yellow-orange

Light purple



Note: The bottom two spots are red-orange and yellow respectively.


2307 A
2310
2307
2311
2316
2317
2304
2318
2315
2314
2313
2305
1689
2306
2312
2308
2309
Rf
50
60
70
80
90
100

10 to 12 in different individuals. In most of these birches there was a bright blue spot at Rf of 0.46 and a yellow-orange spot at Rf 0.50. In all of var. glandulifera chromatograms there were one or more bright purple, purple or dark red-purple spots at Rf's of 0.51-0.63. In six of the eight chromatograms there were bright blue spots at Rf 0.67 and the other two had bright purple (2316) and purple (2311) spots at this Rf. All but one of the chromatograms of var. glandulifera had one or more purple, bright purple and/or reddish purple spots at Rf's of 0.70-0.78. The other chromatogram (2304) had a bright blue and blue-green spot at this Rf. Immediately above the orange-red and yellow spots which were present near the solvent front of all of the chromatograms there were one or more spots which were green to blue-green in six of the chromatograms. The other two had blue (2317) and purple (2310) spots at this Rf. From the number and variation in the spots present in B. pumila var. glandulifera one can conclude that there must have been more separation of the spots in a 24 hour period than was found by Clausen, and that perhaps the atmosphere of the chromatographing cabinet was more saturated.

Clausen (1963) found that his other parental species, Betula papyrifera, produced one bright blue spot at an Rf value of 0.21. The other parental species in the Ponoka bog population is B. resinifera, which had fewer spots (from 8 to 11) than did B. pumila var. glandulifera. One of these birches

(2306) had a chromatogram with a bright blue spot at Rf 0.47. None of the other three had a spot at this Rf, and none had a bright blue spot at the top. This same birch had a red purple spot at Rf 0.50 while numbers 2312 and 2308 had purple spots at this Rf. All four B. resinifera chromatograms gave yellow-orange spots at Rf 0.50-0.56. Two of the four (2306 and 2308) had purple spots at Rf 0.58. The other two had no spot at this Rf. Numbers 2308 and 2309 had yellow-orange spots at Rf 0.66 and the other two had purple and bright purple spots at this Rf. One of the B. resinifera chromatograms (2308) had a bright blue spot at Rf 0.70. All of the B. resinifera chromatograms had two or more purple spots at Rf's 0.72-0.80. Two, 2312 and 2309, had bright purple spots at Rf 0.85 and number 2308 had two spots, blue-green and purple at Rf's 0.84-0.86. There were therefore fewer and less bright spots present in B. resinifera bark chromatograms.

The five hybrid birches which were chromatographed showed great numbers (9 to 14) and great variation in the spots present. There seemed to be more bright spots than in either of the parents except in one of the hybrids (2315) which had no bright spots. Birch 2314 had two bright purple spots and two bright blue spots, number 2313 had three bright blue spots, number 2305 had four bright blue spots, and number 1689 had two bright blue spots. All of the hybrids had a yellow-orange spot at Rf 0.46-0.50 and all had a reddish purple spot at Rf's 0.50-0.56. As expected, the variation in the

hybrids is greater than that in the parental species, but there is also considerable variation present in the bark chromatograms of the parents.

Actual identities of the fluorescing compounds are not shown, nor was it considered feasible for the purposes of the present study to make any attempts to identify them. Clausen (1962, 1963) and Stebbins, *et al*. (1963) also made no attempt to identify fluorescing compounds because it was beyond the scope of their studies.

Extracts of the bark of three of the birches, one of each of the parents and one hybrid (2310, 1689, and 2306) were chromatographed and tested for the presence of sugars with benzidine and for the presence of amino acids with ninhydrin. The results of the sugar test can be seen in Figure 13. The spots near the solvent front seemed to be the same in all three of the birches. *Betula pumila* var. *glandulifera* and *B*. x *uliginosa* had four spots while *B*. *resinifera* had only three. Both parents had gold spots at Rf 0.79 while the hybrid had a light brown spot at this Rf. *B*. *pumila* var. *glandulifera* and the hybrid had dark brown spots at Rf 0.82 and *B*. *resinifera* and the hybrid had greenish brown spots at Rf 0.87 while var. *glandulifera* had a dark brown spot at this Rf. We cannot assume that these spots correspond to the fluorescent spots which are in similar position because it may be that the fluorescent spots are masking the sugar spots. When the same three birches were tested for amino acids, no spots developed on the chromatogram.

FIGURE 13.

Chromatograms of Ponoka bog birch bark sprayed for the presence of sugars.

2310 - *Betula pumila* var. *glandulifera*; 1689 - *B*. x *uliginosa*; 2306 - *B*. *resinifera*.

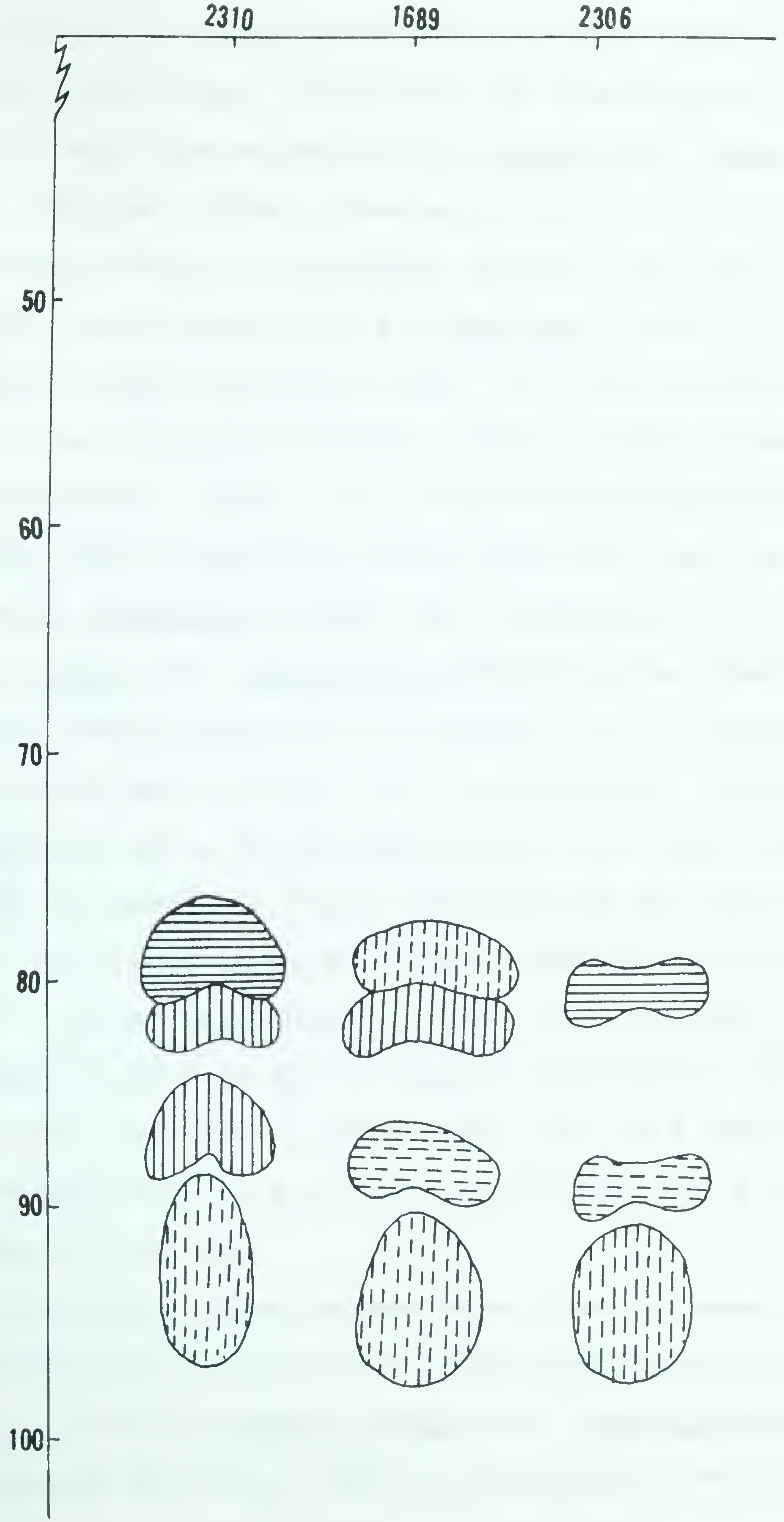
Key

Gold

Dark brown

Light brown

Greenish brown



2310
1689
2306
50
60
70
80
90
100
R_f

Figure 14 presents tracings of chromatograms of leaves of Ponoka bog birches. The first two chromatograms (2310 and 2316) are made from extracts of B. pumila var. glandulifera leaves. The next three chromatograms (2315, 2314, and 1689) are extracts from B. x uliginosa leaves. The last two (2306 and 2309) are extracts from B. resinifera leaves. These are arranged in order of hybrid index. In the following discussion, the color of the spots refers to their fluorescence under ultraviolet light. All of the chromatograms had an orange or light orange spot at Rf 0.20-0.30, and two, a hybrid 2315 and B. resinifera (2309) had a yellow spot at Rf 0.30. Both B. pumila var. glandulifera chromatograms showed purple and light purple spots at Rf 0.51-0.54. At Rf 0.62, 2310 had a bright blue spot and 23.6 had a purple spot. B. resinifera chromatograms had a single spot at Rf 0.62, light purple in 2306 and red purple in 2309. All three of the hybrid chromatograms had purple spots at Rf 0.54, and bright blue spots at Rf 0.59. Two of the hybrid birches, 2315 and 1689, had bright blue spots at Rf 0.64 and the third (2314) had a light purple spot at this Rf. Two of the hybrids (2314 and 1689) had purple spots at Rf 0.74 and the third (2315) had a bright blue spot at this Rf.

When these chromatograms were viewed in ammonia vapor in daylight and in ultraviolet light bright yellow spots became visible. All of the Betula pumila var. glandulifera and hybrid chromatograms had one or two large and nearly continuous spots

FIGURE 14.

Chromatograms of Ponoka bog birch leaves arranged
in order of hybrid index.

Each is marked with the collection number.

Key

Bright blue

Light purple

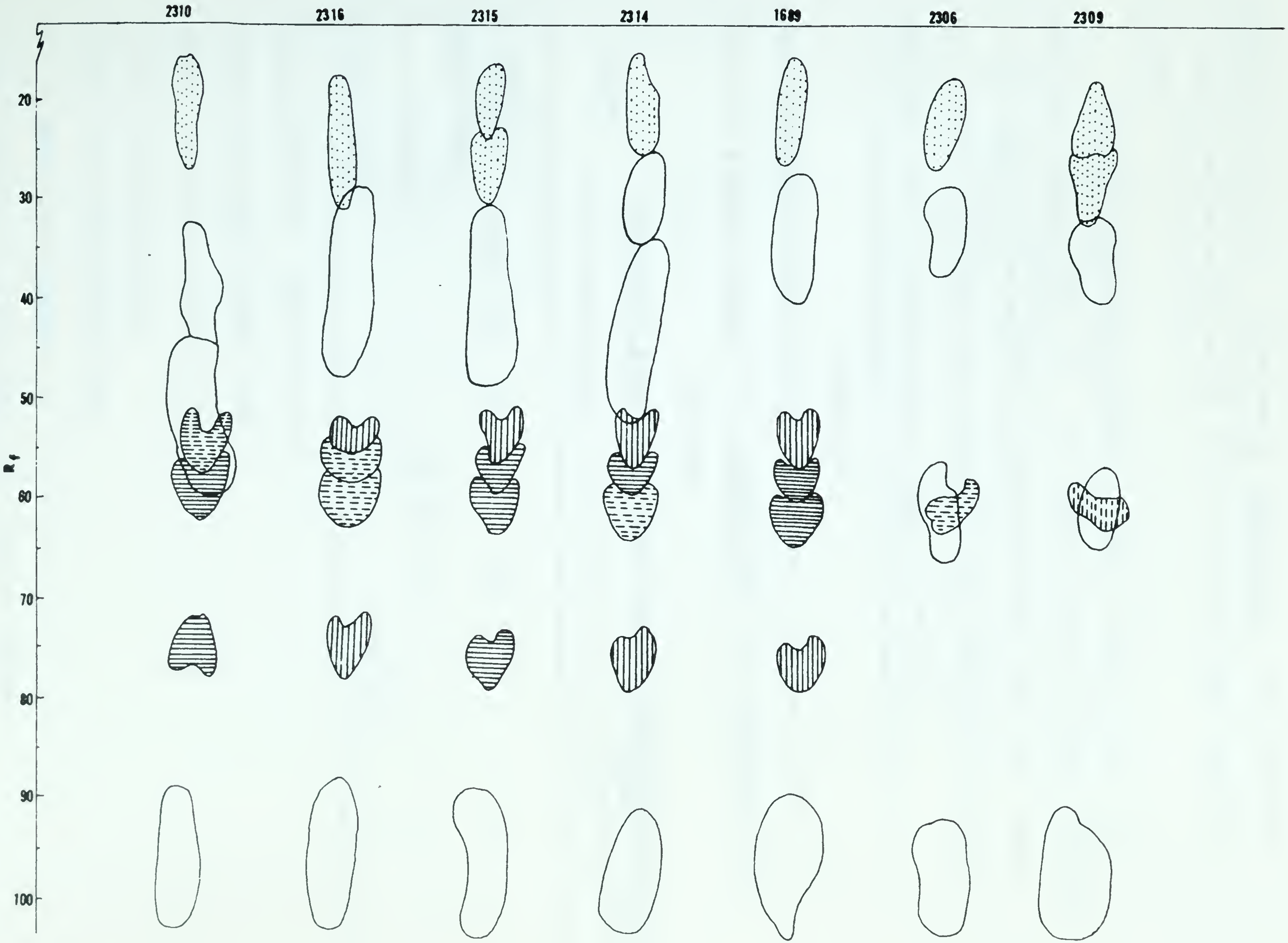
Purple

Red

Yellow-orange

Bright yellow with ammonia vapor

Note: The bottom spot in each chromatogram is deep red.


2310
2316
2315
2314
1689
2306
2309
20
30
40
50
60
70
80
90
100
R_f

from Rf's 0.32-0.52. The two B. resinifera chromatograms had small yellow spots at Rf 0.37-0.38 and bright spots at Rf 0.60.

Certain spots were found to show a correlation with particular taxa (Table 10). It should not be assumed, however, on the basis of the evidence presented here that they represent species specific spots although this could be the case. Additional work is required in order to be sure.

TABLE 10.

The occurrence of fluorescing compounds in chromatograms of leaves of Betula pumila var. glandulifera, B. resinifera and hybrids.

Taxon	Detected substances* and their percentage occurrence								
	pg-1	pg-2	pg-3	h-1	h-2	h-3	r-1	r-2	Number of plants chromatographed
B. pumila var. glandulifera	100	50	50	50		50			2
B. x uliginosa				100	100	67			3
B. resinifera							100	100	2

* pg-1, Rf 0.53, light purple

pg-2, Rf 0.62, bright blue

pg-3, Rf 0.75, bright blue

h-1, Rf 0.54, purple

h-2, Rf 0.59, bright blue

h-3, Rf 0.74, purple

r-1, Rf 0.60, bright yellow in ammonia vapor

r-2, Rf 0.62, red-purple

Chromosome Numbers in Ponoka Bog Birches

Betula resinifera has a chromosome number of 2n = 28 (Plate 15, Fig. 1 and 2). A chromosome number for this species has not been previously reported in the literature. *B. pumila* var. *glandulifera* has a chromosome number of 2n = 56 (Woodworth, 1931). The hybrid birches have chromosome numbers of 2n = 28 - 56. The Ponoka bog individuals for which accurate chromosome number has been determined are as follows:

1685.	*B. resinifera*	2n = 28
1702.	*B. resinifera*	2n = 28
1707.	*B. resinifera*	2n = 28
2168.	*B. resinifera*	n = 14 (M I)
2203.	*B. resinifera*	n = 14 (M I; M II)
2211.	*B. resinifera*	n = 14 (M I)
2213.	*B. resinifera*	n = 14 (M I)
1708.	*B. pumila* var. *glandulifera*	2n = 56
2180.	*B. pumila* var. *glandulifera*	n = 28 (diakinesis)
2216.	*B. pumila* var. *glandulifera* (See Plate 15, Fig. 3 and 4)	n = 28 (M I)
1689.	*B. x uliginosa*	2n = 28*
1701.	*B. x uliginosa*	2n = 56*
2177.	*B. x uliginosa*	n = 21 (M I)
2218.	*B. x uliginosa*	n = 26 (M I)

*These counts are from germinating seed of these hybrid birches, and therefore may or may not be the chromosome numbers for the particular numbered birches.

PLATE 15.

Meiosis in Ponoka bog birches.

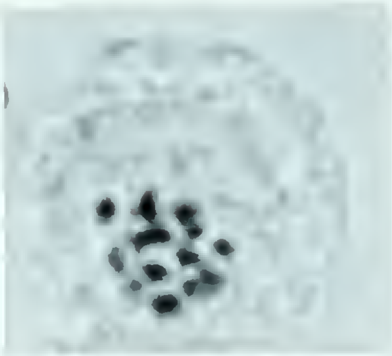
Fig. 1. *Betula resinifera*, M I, n = 14

Fig. 2. *B. resinifera*, M I, drawing of same cell.

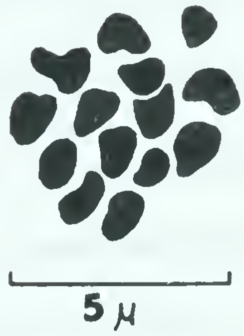
Fig. 3. *B. pumila* var. *glandulifera*, M I, n = 28

Fig. 4. *B. pumila* var. *glandulifera*, M I, drawing

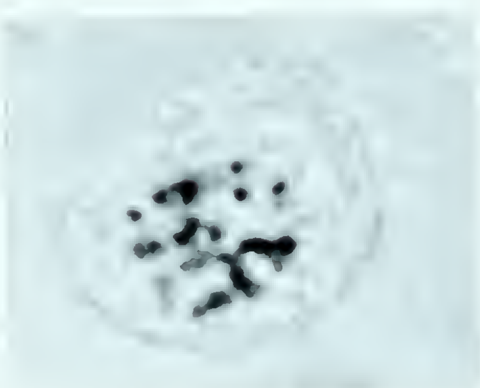
drawing of same cell.



1



2



3

4

Discussion

It has been shown that in the Ponoka bog there are two species, *Betula pumila* var. *glandulifera* with 56 chromosomes and *B. resinifera* with 28 chromosomes which hybridize to form *B.* x *uliginosa* which usually has an intermediate number of chromosomes, though the parental numbers frequently occur. The intermediate characters and discordant variation of the hybrids can be seen in the leaf tracings, drawings of samaras, and polygonal graphs.

It is interesting to note that while in leaf and fruit characters nearly every recombination of parental characters is present, a recombination that might be expected of bark characters, namely light color and non-exfoliating, does not occur. A possible explanation is that it occurs in a non-adaptive genotype and fails to survive in the population.

The hybrid index and pictorialized scatter diagram provide evidence that introgressive hybridization has taken place in the Ponoka bog birches. The frequency histogram illustrates that the intermediates are closer to one parent, *Betula pumila* var. *glandulifera*, than they are to *B. resinifera*. There is a definite break between the hybrids and *B. resinifera* and no break between the hybrids and *B. pumila* var. *glandulifera*. Therefore, introgression seems to be proceeding toward the *B. pumila*

var. glandulifera parent.

Anderson (1951) has pointed out the differences between concordant and discordant variation. A "good" species exhibits concordant variation (= normal pattern of variation), that is, trends are consistent; while it is discordant in the hybrids because there is multiple recombination and virtually every possible variation occurs. It is possible to recognize hybrids because of their discordant variation in comparison to parental forms. However, when discordant variation is found in parental forms, where it is expected that variation will be concordant; there may have been introgression. With an examination of the polygonal graphs and pictorial scatter diagrams one can see evidence of discordant variation, not only in the hybrids, but also in the parental forms, particularly Betula pumila var. glandulifera.

One of the tests which Anderson (1953) has described for recognition of introgression is that sterility, if any, shows up in the intermediates. Since the pollen of Betula resinifera is 97 per cent stained, that of B. pumila var. glandulifera is 93 per cent stained, and that of the hybrids is 79 per cent stained, there is some reduction of stainable cytoplasm in the pollen of the hybrids.

The chromatograms are not an infallible taxonomic tool, but the technique proved to be of value in providing substantiating evidence. The hybrids had more spots in

common with B. pumila var. glandulifera than with B. resinifera, although there was a great deal of variation and several spots which were present in B. resinifera of were present in neither parent were observed.

Clausen (1962) has concluded that introgression in Betula is from the shrubby parent into the tree-sized parent (Betula pumila var. glandulifera to B. papyrifera) and has pointed out that these conclusions agree with other studies in Betula hybrids. For example: Froiland (1952) found evidence of introgression of the shrub B. fontinalis (B. occidentalis) into B. papyrifera in a hybrid swarm in Colorado, and Natho (1959) showed that the shrubby B. humilis was introgressing into two species of trees, B. verrucosa and B. pubescens, in Germany. However, this situation is not present in the Ponoka bog birches, as the shrub, B. pumila var. glandulifera, has been introgressed by the tree, B. resinifera.

However, another suggestion made by Clausen, that the birch of higher ploidy is introgressed by the birch of lower ploidy can be applied here. Since B. resinifera has 28 chromosomes, and B. pumila var. glandulifera has 56 chromosomes, gene flow is from B. resinifera to var. glandulifera. Clausen has shown introgression from B. pumila var. glandulifera (2n = 56) to B. papyrifera (2n = 56?, 70?, or 84?). Froiland (1952) showed introgression from B. fontinalis (2n = 28) to B. papyrifera

(2n = 56?, 70?, 84?). Natho (1959) has shown introgression of _B. humilis_ (2n = 28) into _B. pubescens_ (2n = 56) and also _B. humilis_ (2n = 28) into _B. verrucosa_ (2n = 28). Several authors (Jentys-Szaferowa, 1950; Yurkevich and Gel'tman, 1956; Stern, 1959; Natho, 1959) have also reported introgressive hybridization between _B. verrucosa_ (2n = 28) and _B. pubescens_ (2n = 56). Some backcrossing to _B. verrucosa_ is likely but a majority of authors agree that gene flow is mainly from _B. verrucosa_ to _B. pubescens_. A number of recent publications lend support to this view expressed by workers in the genus _Betula_ that the taxon with the higher chromosome number was introgressed by the one with the lower chromosome number: _Viola lactea_ (n = 29) was introgressed by _V. riviniana_ (n = 20), Moore (1959); Zohary and Nur (1959) have shown one-way gene flow from diploid level to tetraploid level in _Dactylis_; _Digitaria adscendens_ (2n = 54) has apparently been introgressed by _D. sanguinalis_ (2n = 36), Ebinger (1962) and Gould (1963) although neither author specifically mentions this; _Gossypium hirsutum_ (2n = 52) was introgressed by _G. armourianum_ (2n = 26), Brown (1951).

It is difficult to ascertain from recent literature on introgression whether or not this is a more general phenomenon, because chromosome numbers for one or the other of the parents have not been reported: _Quercus macrocarpa_ (2n = 24), and _Q. bicolor_, Bray (1960); _Aesculus_

pavia (2n = 40) and *A. sylvatica*, Hardin (1957); *Carex rostrata* (2n = 82, 76, 60), *C. rotundata*, and *C. paludivagans*, Drury (1956); *Artocarpus altilis* (2n = 56, 81) and *A. mariannensis*, Fosberg (1960); *Juniperus virginiana* (2n = 22, 33) and *J. ashei*, Hall (1952); *Aesculus octandra* (2n = 40) and *A. glabra*, Hardin (1957a); *Acer saccharum* (2n = 26) and *A. nigrum*, Paddock (1961); *Viola affinis* (2n = 54) and *V. sagittata* and *V. papilionacea*, Russell and Risser (1960); *Alnus rugosa* var. *americana* (*A. rugosa*, 2n = 28) and *A. serrulata*, Steele (1961); *Quercus chrysolepis* (2n = 24) and *Q. dunnii*, Tucker and Haskell (1960). No case among previous papers on introgression has come to the attention of the author where the taxon with larger chromosome number introgresses the taxon with smaller chromosome number. The evidence would seem to point to the fact that in *Betula*, when other factors are equal, the species with the lower degree of ploidy introgresses the species with higher degree of ploidy.

BETULA GLANDULOSA X *BETULA PUMILA* VAR. *GLANDULIFERA* (*B.* x *sargentii*)

In several areas of the Rocky Mountains and the foothills were found birches which were impossible to identify with the ordinarily used key characters (Butler, 1909; Moss, 1959). In some respects these birches resembled *Betula pumila* var. *glandulifera*, in others they resembled *B. glandulosa*, and in still others they were intermediate (Plate 16). It was thought likely that hybridization was responsible for the situation in these birch species. Samples of the taxa were collected from several areas where they were found growing together. In the analysis the material was pooled and analyzed as a single heterogeneous population. The population consisted of 135 individuals.

Characters of Gross Morphology Used in the Analysis

A summary of the morphological characters used in the analysis is in Table 11.

Various intermediate characters were recognized, and these various categories can be seen in Table a4 and the key to Figure a24.

Variation in the leaves of this population is illustrated in Figure a22. Bracts were not used in the analysis because so much variability was found, even within the same catkin. Variation in bracts and samaras within the population is shown in Figure a23.

PLATE 16

Photographs of Betula x sargentii.

Fig. 1. Number 2319, Campsite near Edson, Alberta, July 28, 1963.

Fig. 2. Several of the Betula x sargentii hybrids, Obed Campsite, near Obed, Alberta, July 28, 1963.

TABLE 11.

Gross morphological characters of *Betula glandulosa* and *B. pumila* var. *glandulifera* used in the analysis.

Betula glandulosa	*B. pumila* var. *glandulifera*
Branchlets densely glandular	Branchlets sparsely glandular
Leaves round	Leaves obovate
Leaves round at base	Leaves cuneate at base
Leaves less than 2 cm long	Leaves more than 2.5 cm long
Leaves less than 1.5 cm wide	Leaves more than 1.8 cm wide
Leaf margin crenate	Leaf margin crenate-serrate
Less than 10 crenations on one leaf margin	More than 14 crenations on one leaf margin
3-4 pairs of lateral leaf veins	More than 5 pairs of lateral leaf veins
Fruiting catkins less than 1 cm long	Fruiting catkins more than 1 cm long
Wings of samara narrower than body and less than ½ as wide	Wings of samara narrower than body but more than ½ as wide

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the ten selected characters on each of the radii of the graphs are shown in Figure a24. A selected group of representative polygons is shown in Figure a25.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table a4. In

each, the index value of 0 is typical of one extreme in the character, and the index value of 2 or 3 is typical of the other extreme. Variation from these extremes is indicated by the intermediate values. A typical *B. glandulosa* index range is 0-4 while a *B. pumila* var. *glandulifera* index range is 17-21.

The total index value for each individual was determined, and a bar graph was constructed upon which the hybrid index values were plotted against their frequencies (Figure 17). It can be seen that two peaks are present, one beginning within the arbitrary *B. glandulosa* range, but extending into the intermediate range of 10 or 11, and another beginning within the *B. pumila* var. *glandulifera* range, but extending into the intermediate range of 11 or 12.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of five leaves and the number of pairs of leaf veins. Each individual was plotted (Figure 18).

Germination Data

Germination tests were made of the fruits of *Betula pumila* var. *glandulifera*, *B. glandulosa* and *B.* x *sargentii*. The fruits were tested without prior examination to see if they contained seed. There is some evidence of reduction of fertility in the hybrids. The results are presented in Table 12.

FIGURE 17.

Frequency of hybrid index values of *Betula glandulosa*, *B. pumila* var. *glandulifera*, and hybrids.

Frequency
13
12
11
10
9
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Betula glandulosa
Betula pumila var. glandulifera
Hybrid index values

FIGURE 18.

Pictorial scatter diagram of *Betula glandulosa*, *B. pumila* var. *glandulifera* and hybrids

Key

Leaf shape

Round

Elliptic

Obovate

Leaf base

Round

Round-cuneate

Cuneate

Branchlet gland density

Dense

Scattered

Sparse

Leaf margin

Crenate

Crenate-serrate

Serrate

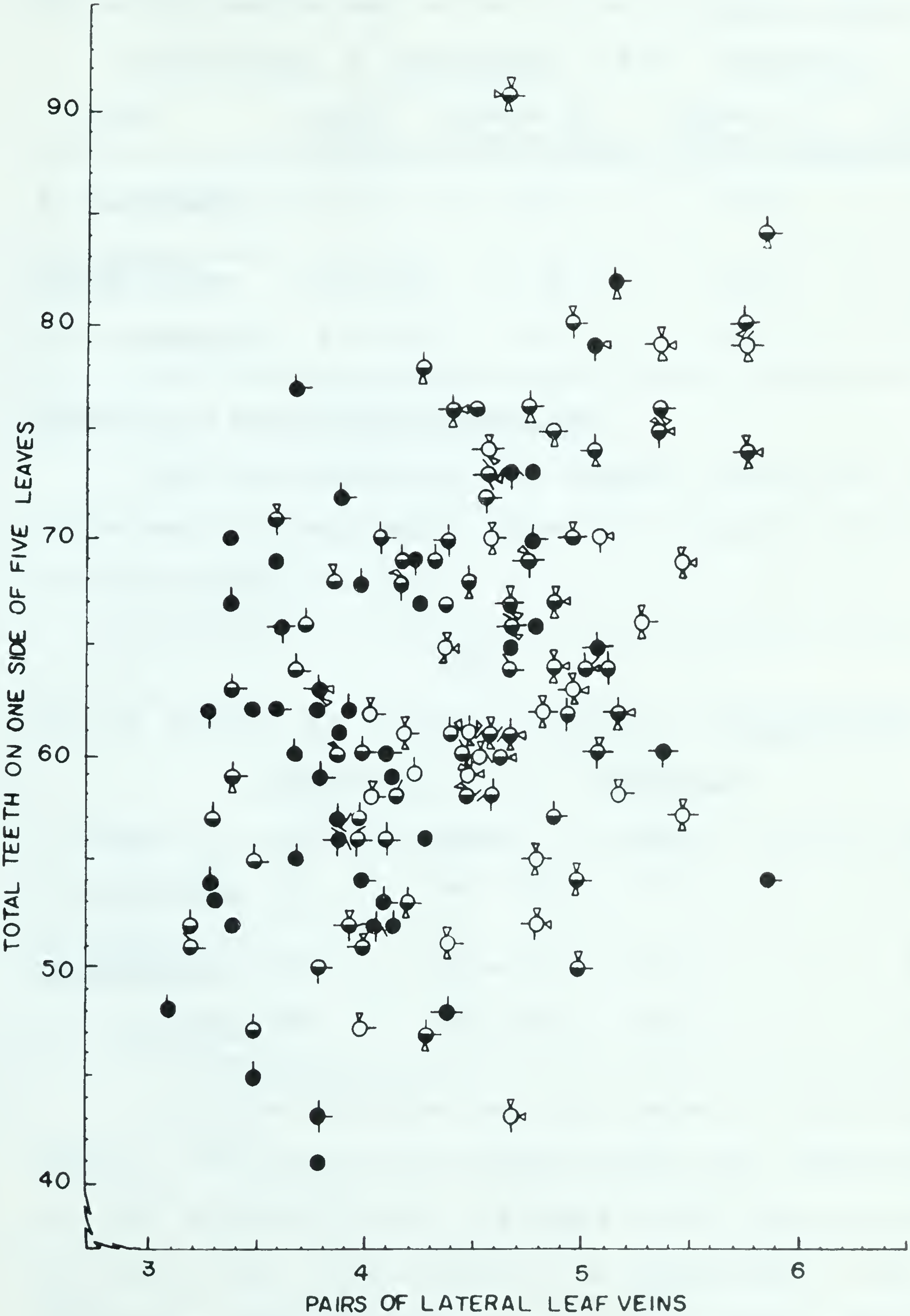
Leaf length

Less than 2 cm

2 - 2.5 cm

More than 2.5 cm

Note: When necessary to avoid overlapping, appendages are bent.



TOTAL TEETH ON ONE SIDE OF FIVE LEAVES
90
80
70
60
50
40
3
4
5
6
PAIRS OF LATERAL LEAF VEINS

TABLE 12.

Percentage germination of the fruits of _Betula pumila_ var. _glandulifera_, _B. glandulosa_ and _B. x sargentii_.

Taxon	Hybrid indices	Number of individuals	Number of seeds planted	Percentage germination
B. glandulosa	0 - 5	11	254	20.5%
B. pumila var. _glandulifera_	16 - 21	4	100	40.0%
B. x sargentii	6 - 15	26	503	16.9%

Stomata and Pollen Grain Morphology

The distribution of mean stomatal lengths of the three taxa is presented in Table a5. A summary of stomatal size data is in Table 13.

TABLE 13.

Size of stomata (μ) in _Betula pumila_ var. _glandulifera_, _B. glandulosa_ and _B. x sargentii_.

Taxon	N	Range	Mean	S.D.
B. glandulosa	24	14.7-24.7	20.0	2.44
B. pumila var. _glandulifera_	14	18.9-29.7	24.8	2.77
B. x sargentii	89	16.3-28.1	22.3	8.51

A greater variation was thus found in hybrid stomatal length. The analysis of variance (Table 14) demonstrated that the difference among the means of the three taxa was not significant. Since there is no significant F, the application of Duncan's test is not necessarily warranted.

However, when applied, it was found that no mean was significantly different from any other.

TABLE 14.

Analysis of variance in stomatal length in Betula pumila var. glandulifera, B. glandulosa and hybrids.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	133.108	2	66.554	1.249
Within taxa	6610.092	124	53.307	
Total	6743.200	126		

Pollen of Betula pumila var. glandulifera from these populations ranges from 20.9 μ to 22.2 μ with a mean of 21.6 μ with a sample too small to analyze; B. x sargentii pollen ranges from 15.4 μ to 22.6 μ with a mean of 19.9 μ and a standard deviate of 3.20; and B. glandulosa pollen has a mean of 16.5 μ without a sample large enough for analysis. One can only say that there is a tendency for the pollen of the hybrid, B. x sargentii, to be smaller than that of B. pumila var. glandulifera, and to be larger than that of B. glandulosa. There is also considerable variation in the size of B. x sargentii pollen.

Chromosome Numbers

Betula glandulosa has a chromosome number of 2n = 28 (dePoucques, 1949; Packer, 1964) (Plate 19, Figures 1 and 2). B. pumila var. glandulifera has a chromosome number of 2n = 56

PLATE 19.

Chromosome numbers of _Betula glandulosa_, _B. pumila_ var. _glandulifera_, and hybrid.

Fig. 1. _Betula glandulosa_, 2n - 28

Fig. 2. _B. glandulosa_, drawing of same cell.

Fig. 3. _B. pumila_ var. _glandulifera_, 2n - 56

Fig. 4. _B. pumila_ var. _glandulifera_, drawing of same cell.

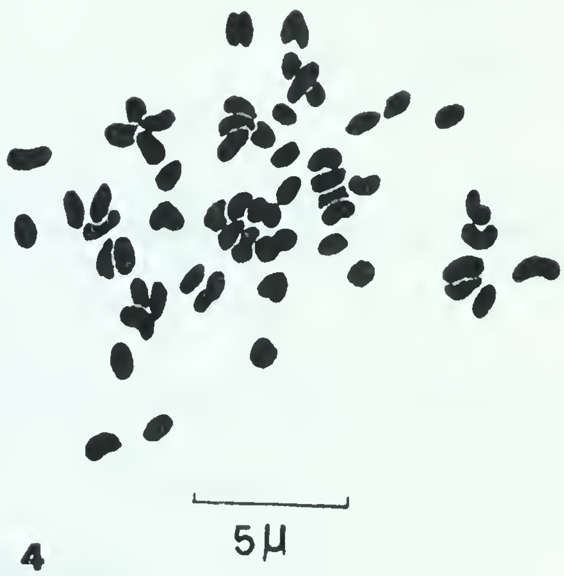
Fig. 5. _B. x sargentii_, 2n - 48

Fig. 6. _B. x sargentii_, drawing of same cell.

1

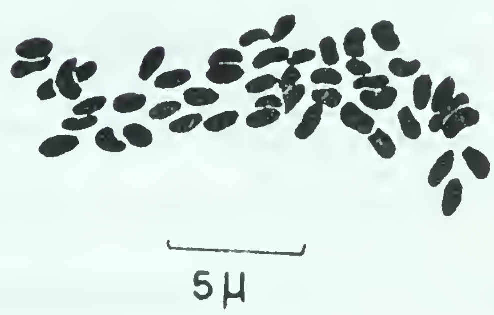
2

3



4

5



6

(Woodworth, 1931) (Plate 19, Fig. 3 and 4). The hybrid usually has chromosome numbers intermediate between those of the parental species (2n = 28 - 56). The individuals for which accurate chromosome number determinations have been made are as follows:

1723.	Betula x sargentii	2n = 42*
1726a.	B. x sargentii	2n = 49*
1726b.	B. x sargentii	2n = 56*
1726c.	B. x sargentii	2n = 48*

(Plate 19, Fig. 5 and 6)

* These counts are from germinating seed of these hybrid birches, and therefore may or may not be the chromosome numbers for the particular numbered birches.

Several counts were made of chromosome numbers during Meiosis II in Betula x sargentii (2238). The number of chromosomes in the meiospores were as follows: 21, 23, 14, 15, 18, and 20. In a cross between Betula pumila var. glandulifera and B. glandulosa, the number of chromosomes in the pollen mother cell would be 42. It is probable that in these hybrids fourteen pairs are formed and the other fourteen chromosomes move in either direction or pair among themselves (as described by Woodworth, 1931). Thus chromosome numbers of n = 14 to n = 28 are likely to occur.

Discussion

It has been shown that in the Rocky Mountains and in the foot hills there are two species, *Betula glandulosa* with 28 chromosomes and *B. pumila* var. *glandulifera* with 56 chromosomes which hybridize to form *B.* x *sargentii* which usually has an intermediate number of chromosomes. The intermediate variation in characters of the hybrids can be seen in the leaf tracings, drawings of samaras, and polygonal graphs.

The hybrid index and pictorialized scatter diagram provide evidence that introgressive hybridization has taken place in the Rocky Mountain bog and dwarf birches. The variation in *Betula glandulosa* is all in the direction of *B. pumila* var. *glandulifera* and the variation in the latter is all in the direction of the former. According to Anderson and Rudolph (1956), introgression is the only known evolutionary force which produces population variation patterns of this kind. Less concordant variation is found in *B. pumila* var. *glandulifera* which shows gene flow from *B. glandulosa* to *B. pumila* var. *glandulifera*. There is much evidence that introgression is in both directions, especially the presence of two peaks in the histogram; but also in examining the histogram we find that 19 of the birches are within the arbitrary range of *B. glandulosa* and only 9 are within the range of *B. pumila* var. *glandulifera*. Since the samples were rather large

and were randomly selected, it appears that the latter has been influenced by gene flow more than has the former. Other evidence which shows the introgression of B. pumila var. glandulifera is the mean stomatal length which is 4 μ shorter than the average of B. pumila var. glandulifera from the Ponoka bog (page 139). It appears that nearly all of the B. pumila var. glandulifera has received some genes from B. glandulosa.

Tucker (1960) has commented that if one species shows more variation than does another species and if the variation is in the direction of the second species, it is the result of introgression. Certain of the parental species may virtually lose their identity in particular areas. This is what has happened in Betula glandulosa crossed with B. pumila var. glandulifera. The foothills region in the Rocky Mountains and other fairly intermediate habitats have as dominant birch, not B. glandulosa or B. pumila var. glandulifera, but B. x sargentii. Even with the large number of birches belonging to these taxa collected at random in these regions (135), very few were found which could be considered typical B. glandulosa or B. pumila var. glandulifera.

Introgression seems to be in the direction of higher ploidy as found by Clausen (1962), Froiland (1953), Natho (1959), Yurkevich and Gel'tman (1956), Jentys-Szaferowa

(1950), and Stern (1959). Gene flow is from B. glandulosa (2n = 28) to B. pumila var. glandulifera (2n = 56).

BETULA GLANDULOSA X BETULA FONTINALIS (*B. x eastwoodae*)

In several areas of the Rocky Mountains and the foothills, it was established that *Betula fontinalis* and *B. glandulosa* were present. Also present were individuals fitting the description of *B. x eastwoodae* which was reported by Sargent (1922) as being prevalent in the Jasper National Park area. Due to the wide variation in the species and intermediates found, hybridization was suspected and it might also be noted that various authors (Hultén, 1944; Anderson, 1942; and Krüssmann, 1962) have suggested that *B. x eastwoodae* was a hybrid. Studies were undertaken to test this hypothesis. Samples of the taxa were collected from several areas where they were found growing together. In the analysis the material, consisting of 134 individuals, was pooled and analyzed as a single population.

Characters of Gross Morphology Used in the Analysis

A summary of the morphological characters used in the analysis is in Table 15.

Various intermediate characters were recognized and these various categories can be seen in Table a6 and in the key to Figure a27.

It was found that base of leaves, even though it has been used as a distinguishing character in the past (Butler, 1909), was of doubtful value, since the range of variation within the parental species was so great. Even so, it was decided to include the character because its polygonal graph

could possibly show up some association of the type of leaf base with some of the other characters used. Three types of leaf base were recognized: (1) truncate; (2) round-cuneate; and (3) cuneate. Variation in the leaves is illustrated in Figure a26.

TABLE 15.

Gross morphological characters of *Betula glandulosa* and *B. fontinalis* used in the analysis.

Betula glandulosa	*Betula fontinalis*
Branchlet glands whitish	Branchlet glands reddish
Leaves dull	Leaves shiny
Leaves less than 2 cm long	Leaves more than 3 cm long
Leaves less than 1.5 cm wide	Leaves more than 2 cm wide
Leaves round to ovate	Leaves rhomboidal to broadly ovate
Leaves round at apex	Leaves acute at apex
Leaves round to round-cuneate at base	Leaves truncate to rounded at base
Leaf margin crenate	Leaf margin serrate to doubly-serrate
Less than 10 crenations on one leaf margin	More than 20 crenations on one leaf margin
3-4 pairs of lateral leaf veins	More than 5 pairs of lateral leaf veins

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the eight selected characters on each of the radii of the graphs are shown in

Figure a27. A selected group of representative polygons is shown in Figure a28.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table a6. In each, the index value of 0 is typical of one extreme in the character, and the index value of 2 or 3 is typical of the other extreme. Variation from these extremes is indicated by the intermediate values. A typical *B. glandulosa* range is 0-4 while a *B. fontinalis* index range is 18-23. The total index value for each shrub was determined, and a bar graph was constructed upon which the hybrid index values were plotted against their frequencies (Figure 20). It can be seen that there are approximately three peaks present, one beginning within the arbitrary *B. glandulosa* range, another beginning within the *B. fontinalis* range, and a group of intermediate individuals which have hybrid index values mostly from 8-12.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of five leaves and the average length of leaf in cm (Figure 21).

Germination Data

Germination tests were made of the fruits of *Betula fontinalis*, *B. glandulosa*, and *B.* x *eastwoodae* without prior examination to see if they contained seed. There

FIGURE 20.

Frequency of hybrid index values of *Betula glandulosa*, *B. fontinalis* and hybrids.

Key

Eastwood 271-88, isotype of *Betula eastwoodae* Sarg.

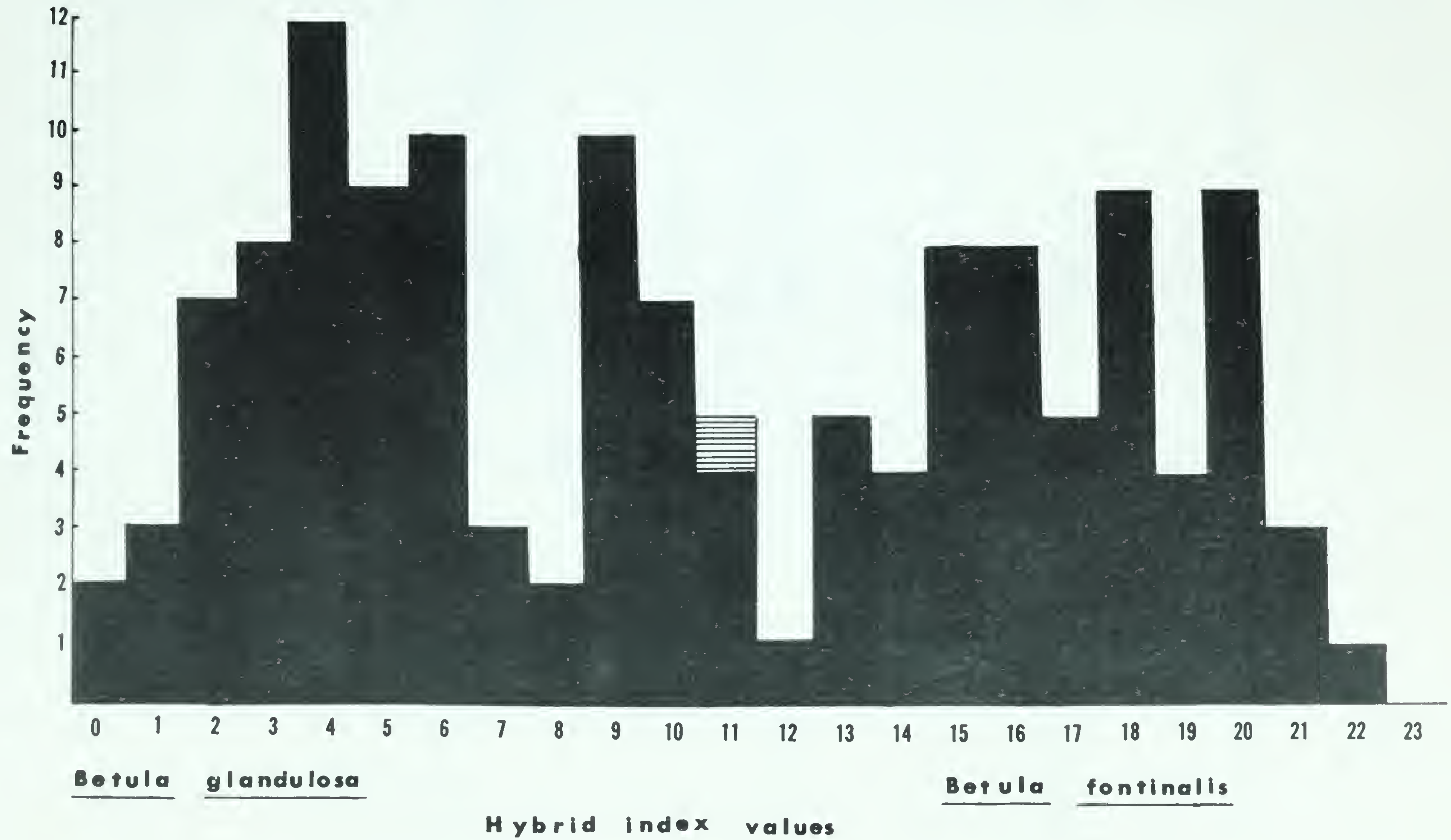

Frequency
12
11
10
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
Betula glandulosa
Betula fontinalis
Hybrid index values

FIGURE 21.

Pictorial scatter diagram of _Betula glandulosa_, _B. fontinalis_, and hybrids.

Key

Branchlet gland color

Red

Yellow

White

Leaf tip

Acute

Round-acute

Round

Leaf margin

Doubly-serrate

Serrate

Serrate-crenate

Crenate

Leaf veins

More than 5 pairs

4-5 pairs

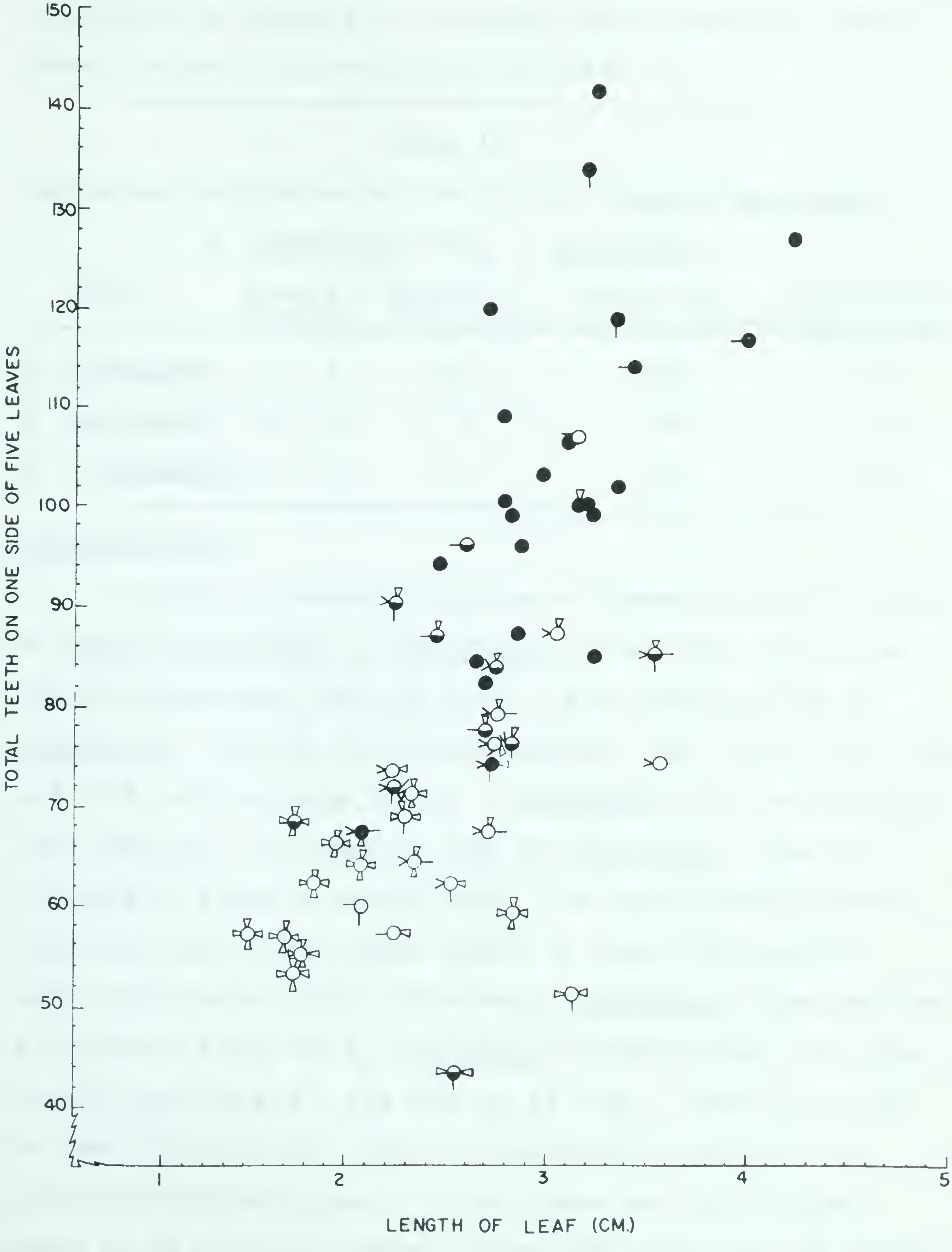
3-4 pairs

Note: When necessary to avoid overlapping, appendages are bent.

Leaf surface

Glandular leaves

No glandular leaves


TOTAL TEETH ON ONE SIDE OF FIVE LEAVES
150
140
130
120
110
100
90
80
70
60
50
40
1
2
3
4
5
LENGTH OF LEAF (CM.)

appears to be evidence of increased hybrid fertility among these birches. The results are in Table 16.

TABLE 16.

Percentage germination of the fruits of Betula fontinalis, B. glandulosa and B. x eastwoodae.

Taxon	Hybrid indices	Number of individuals	Number of seeds planted	Percentage germination
B. glandulosa	0 - 4	14	298	15%
B. fontinalis	18 - 23	2	100	9%
B. x eastwoodae	5 - 17	8	176	27%

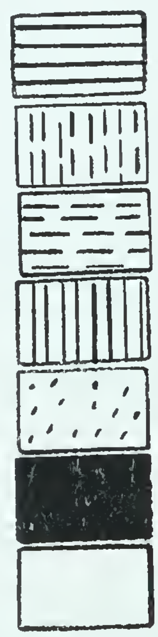
Chromatography

Figure 22 presents tracings of chromatograms of leaves of Betula glandulosa, B. fontinalis and hybrids. The first two chromatograms, 1912 and 1910, are of extracts from B. glandulosa; the next five chromatograms, 1901, 1897, 1900, 1895, and 1907, are extracts from B. x eastwoodae and the last two, 1913 and 1911, are extracts from B. fontinalis. They are arranged in order of hybrid index. In the following discussion the color of the spots refers to their fluorescence under ultraviolet light. The two B. glandulosa chromatograms are identical and the B. fontinalis chromatograms were alike except that one had a red spot at Rf 0.41. However, as can be seen in Figure 22, there is considerable variation in the hybrid chromatograms. All of these had light yellow spots at Rf 0.32-0.34 except number 1895 which had two yellow

FIGURE 22.

Chromatograms of _Betula_ _glandulosa_, _B_. _fontinalis_ and hybrid leaves arranged in order of hybrid index. Each is marked with the collection number.

Key



Bright blue

Red

Light purple

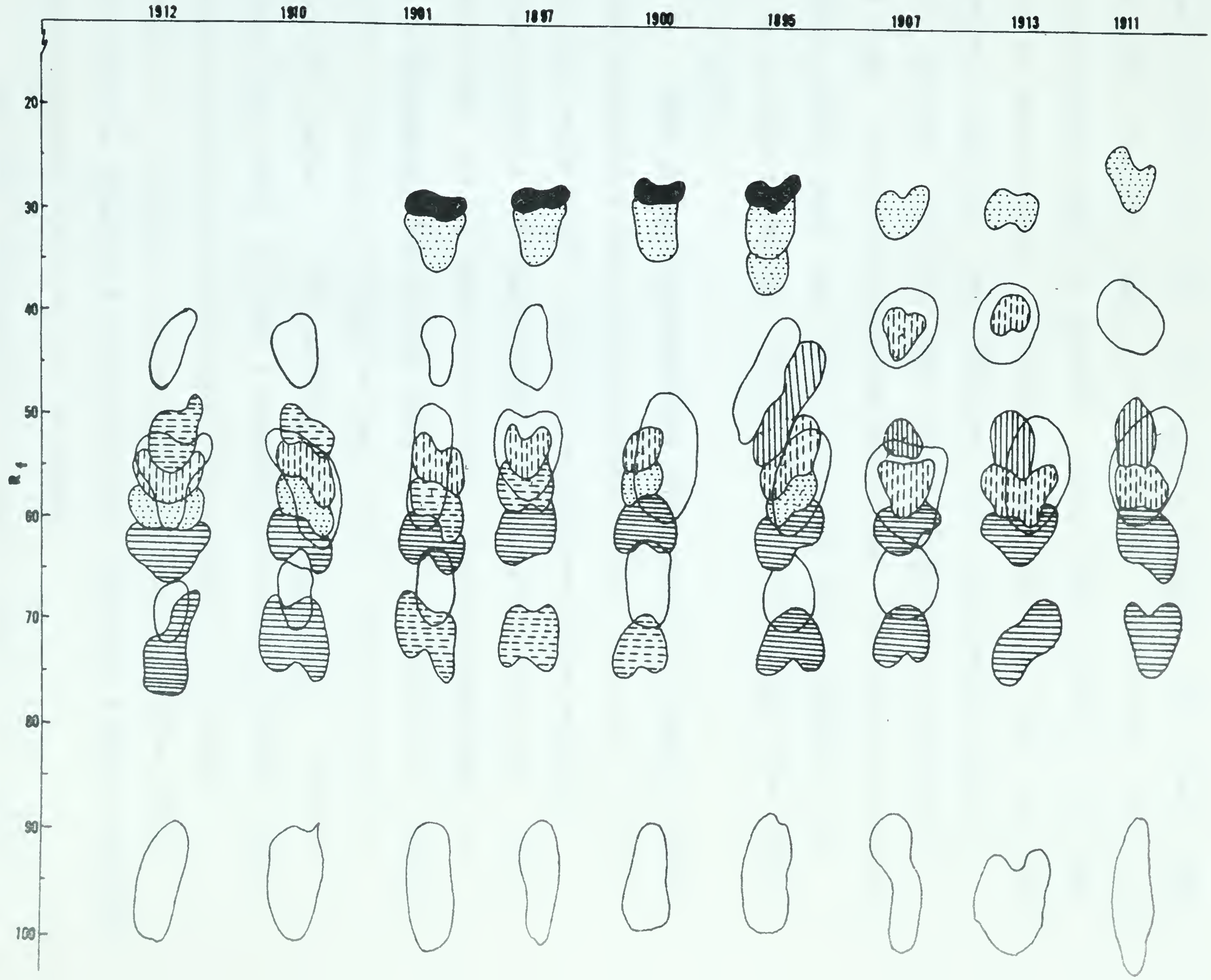
Purple

Yellow

Dark red-purple in ammonia vapor

Bright yellow in ammonia vapor

The spot at Rf 0.95-1.00 in each chromatogram is deep red.



1912
1910
1901
1897
1900
1895
1907
1913
1911
20
30
40
50
60
70
80
90
100
R_f

spots at Rf 0.32-0.38. Four of the hybrids, 1901, 1900, 1895, and 1907, had red spots at Rf 0.54-0.57. The other, 1897, had a dark purple spot at this Rf. Two, 1901 and 1897, had light purple spots at Rf 0.57-0.60 and two, 1900 and 1895 had yellow spots at this Rf. Two, 1895 and 1907, had purple spots at Rf 0.48-0.51, and one, 1907, had in addition a red spot at Rf 0.42. All of the hybrids had bright blue spots at Rf 0.62. Three, 1901, 1897, and 1900, had light purple spots at Rf 0.73 and the other two, 1895 and 1907, had bright blue spots at this Rf.

When these chromatograms were viewed in ammonia vapor, dark purple-red spots were present at Rf 0.29 in all of the hybrids except 1907. All of the birches chromatographed except hybrid 1900 had bright yellow spots at Rf 0.42. All had bright yellow spots at Rf 0.55. _Betula glandulosa_ and _B. x eastwoodae_ had yellow spots at Rf 0.69 except for hybrid 1897, in which was found no spot of any color at this Rf. In this respect it was similar to _B. fontinalis_. Certain spots were found to show a correlation with particular taxa. These spots were numbered and the results can be seen in Table 17. It should not be assumed however, on the basis of evidence presented here that they represent species specific spots although this may be the case.

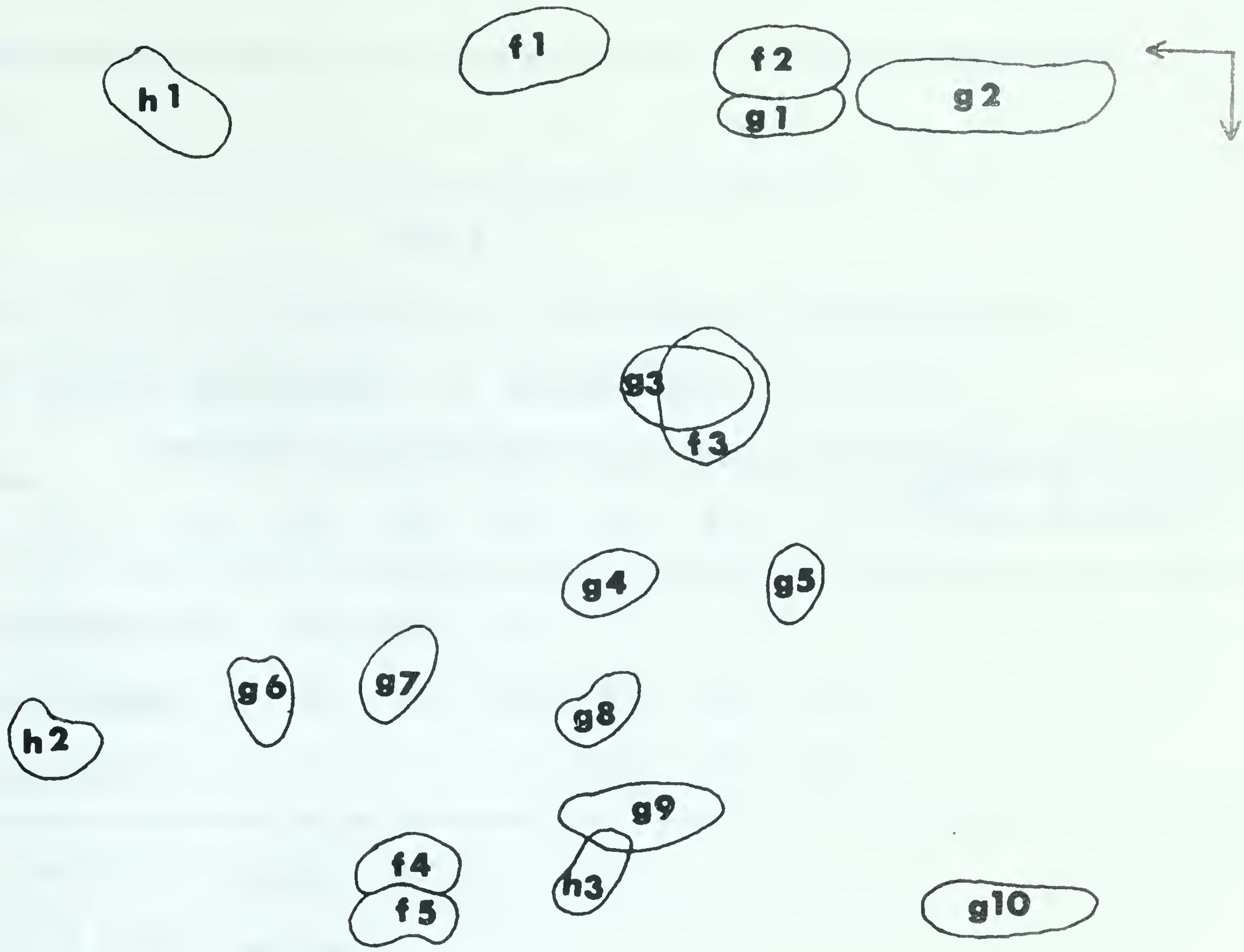
Two way chromatograms of four of these birch individuals showed additional taxon-correlated spots. Figure 23 is a composite diagram showing these spots only, that is, not

FIGURE 23.

Composite diagram of two-way chromatograms of *Betula glandulosa*, *B. fontinalis*, and hybrids, showing only taxon-correlated spots.

The colors of these spots are listed below:

g-1, orange-yellow	g-10, light yellow
g-2, light purple	h-1, faint dark purple
g-3, light red	h-2, dark blue-green
g-4, light red	h-3, purple
g-5, light red	f-1, orange
g-6, purple	f-2, bright yellow
g-7, light purple	f-3, red
g-8, purple	f-4, light purple
g-9, light purple	f-5, light purple


h1
f1
f2
g1
g2
g3
f3
g4
g5
g6
g7
g8
h2
g9
f4
h3
f5
g10

including spots which were common to all birches chromatographed.

TABLE 17.

The occurrence of fluorescing compounds in chromatograms of *Betula fontinalis*, *B. glandulosa* and hybrids

Taxon	Detected substances* and their percentage occurrence							
	g-1	g-2	g-3	h-1	f-1	f-2	f-3	Number of plants chromatographed
B. glandulosa	100	100	100					2
B. x *eastwoodae*		40	80	80	100	20	40	5
B. fontinalis					100	50	100	2

* g-1, Rf 0.53, light purple

g-2, Rf 0.60, yellow

g-3, Rf 0.67, bright yellow in ammonia vapor

h-1, Rf 0.29, dark red-purple in ammonia vapor

f-1, Rf 0.30, yellow

f-2, Rf 0.42, red

f-3, Rf 0.55, purple

Chromosome Numbers

Betula glandulosa has a chromosome number of 2n = 28 (dePouques, 1949; Packer, 1964). *B. fontinalis* has a chromosome number of 2n = 28. This count was first reported by Woodworth (1931) for *B. fontinalis* var. *piperi*. The hybrid birch, *B.* x *eastwoodae*, has the same chromosome number as the parents (2n = 28).

Discussion

The intermediate characters and variation of *Betula* x *eastwoodae* can be seen in the leaf tracings, polygonal graphs, and hybrid index.

Betula fontinalis and *B. glandulosa* are found in similar habitats, and are often found growing together in association with their hybrid (*B.* x *eastwoodae*). In the random sampling of five areas, *B. glandulosa*, *B. fontinalis* and *B.* x *eastwoodae* were growing a few feet apart and were found to occur in the following frequencies: 36, 28, and 36 per cent. The hybrids appear to back-cross to either parent with equal frequency, and although introgression has taken place, neither parent has been introgressed more than the other. Among recent papers in which some aspects of introgression are discussed there are many in which the chromosome number is the same in the hybridizing species. Some of these show introgression in both directions as has been found in *B. fontinalis* x *B. glandulosa*: *Typha latifolia* x *T. angustifolia* (2n = 30), Fassett and Calhoun (1952); hybrids among *Stipa columbianum*, *S. californica*, *S. occidentalis* and *S. elmeri* (2n = 36), Johnson (1962); *Picea glauca* x *P. engelmannii* (2n = 24), *Pinus radiata* (2n = 24) x *P. muricata* (2n = 24?), Newcomb (1959). Others which have the same chromosome number show gene flow in one direction, mostly influenced by the environment favoring one or the other of the parents.

Some examples are: *Betula humilis* into *B. verrucosa* (2n = 28), Natho (1959); *Populus grandidentata* into *P. tremuloides* (2n = 38), Barnes (1961); *Pinus jeffreyi* into *P. ponderosa* (2n = 24), Haller (1959); and *Juniperus scopulorum* into *J. virginiana* (2n = 22, 33 also reported for *J. virginiana*), Hall (1952).

It has been suggested by Hultén (1944), Anderson (1942), and Krüssmann (1962) that *Betula* x *eastwoodae* is a hybrid of *B. resinifera* (*B. papyrifera* var. *humilis*) with *B. glandulosa*. Sargent, who originally described this birch from material collected near Dawson, Yukon Territory by Alice Eastwood, said of this species "....forming jungles with *Betula glandulosa* Michx., *B. alaskana* Sarg. (*B. resinifera* Britton), and various Willows; and as a large shrub in Jasper Park near Jasper, Alberta." From this information subsequent authors have assumed that *B.* x *eastwoodae* was a hybrid of the two birches that Sargent listed. Sargent, however, had described *B.* x *eastwoodae* as a species, and was merely describing the associates of this species. Further, he was clearly aware that *B. fontinalis* occurs in this area as he had referred to this species a number of Eastwood's Dawson collections. In addition Sargent said that *B.* x *eastwoodae* is a common species in Jasper National Park near Jasper, Alberta where *B. resinifera*, one of the previously presumed parents, does not occur. In this

locality the swarms are made up of _B. glandulosa_ and _B. fontinalis_. Since _B. fontinalis_ is also commonly found near Dawson, Yukon Territory, and since the isotype of _B. x eastwoodae_ fits into the range of variation of the hybrids between _B. glandulosa_ and _B. fontinalis_, Figures a28 and 20, it is evident that the parents of _B. x eastwoodae_ are these two species.

BETULA FONTINALIS X BETULA PAPYRIFERA (B. x utahensis)

In several areas of the Rocky Mountains and the foothills were found birches which were not easily identified using the usual key characters (Butler, 1909; Moss, 1959). The area referred to here as Thunder Hill is the Thunder Hill Campsite near Columbia Lake, B. C. (elevation 2777').

It was established that Betula fontinalis and B. papyrifera were present. Also, several individuals which could be identified as B. x andrewsii (Plate a10), B. subcordata (Plate a13), B. montanensis (Plate a12), and B. utahensis (Plate a9) were found. Due to the wide variation in the species and intermediates found, hybridization was suspected. Therefore a study of these birches was undertaken and samples of the taxa were collected from Thunder Hill. The 34 individual birches were treated as a single heterogeneous population.

Characters of Gross Morphology Used in the Analysis

A summary of the morphological characters used in the analysis are in Table 18.

Various intermediate categories were recognized and these can be seen in Table a7 and the key to Figure a30. Variation in the leaves of this population is illustrated in Figure a29.

TABLE 18.

Gross morphological characters of *Betula fontinalis* and *B. papyrifera* used in the analysis.

Betula fontinalis	*Betula papyrifera*
Bark dull brown	Bark beige-white, silvery
Bark non-exfoliating	Bark exfoliating
Branchlets glandular	Branchlets not glandular
Leaves glandular	Leaves pubescent below
Leaves 3-4 cm long	Leaves more than 5 cm long
Leaves less than 3.5 cm wide	Leaves more than 4 cm wide
Leaves rhomboidal to broadly ovate	Leaves broadly ovate
Leaves acute	Leaves acuminate
Leaves truncate at the base	Leaves cuneate at the base
Leaves serrate margined	Leaves doubly-serrate margined
20-30 serrations on one leaf margin	30-40 serrations on one leaf margin
5-6 pairs of lateral leaf veins	More than 7 pairs of lateral leaf veins
Petiole about 1 cm long	Petiole about 2 cm long
Fruiting catkins less than 2 cm long	Fruiting catkins more than 3 cm long
Fruiting catkins less than 1 cm wide	Fruiting catkins more than 1 cm wide

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the characters on each of the eight radii of the graphs are shown in Figure a30.

A selected group of representative polygons are shown in Figure a31.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table a7. For each character, the index value of 0 is typical of one extreme in the character, and the index values of 2,3, or 4 are typical of the other extreme. Variation from these extremes is indicated by the intermediate values. The hybrid index range of 0-4 was arbitrarily selected for *B. fontinalis* and that of 21-25 selected for *B. papyrifera*.

The total index value for each shrub and tree was determined from the individual sets of measurements, and a bar graph was constructed upon which the hybrid index values were plotted against their frequencies (Figure 24). The Celestine Lake population (page 198) was included. Various type specimens and representative trees from the *B. x andrewsii* population of Colorado were also analyzed and included in the Figure. It can be seen that there is a peak at hybrid index value 16, and that very few of the birches in the population are within the arbitrary ranges of either parent.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of five leaves and the number of pairs

FIGURE 24.

Frequency of hybrid index values of *Betula fontinalis*, *B. papyrifera* and hybrids.

Key

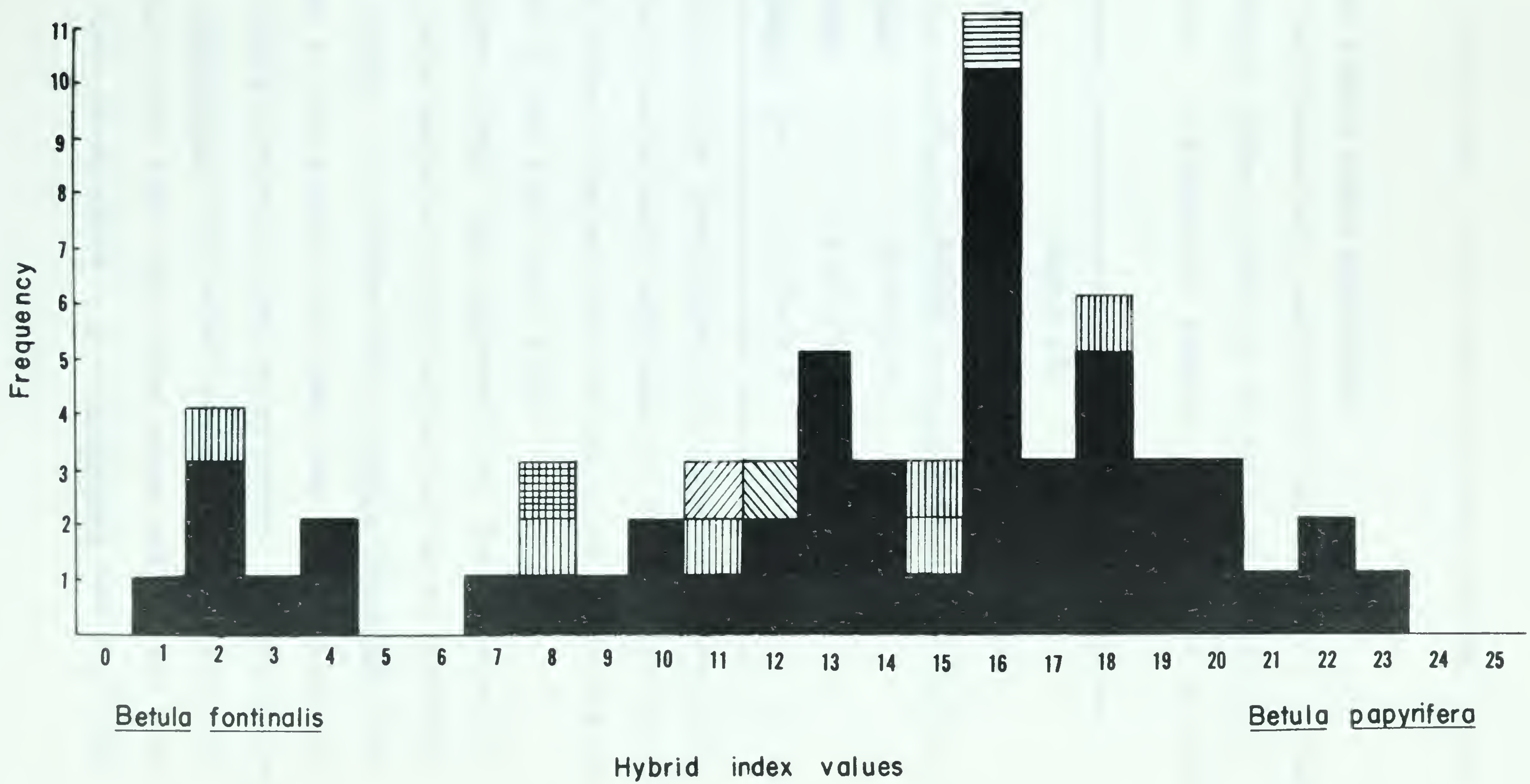
B. x *andrewsii* Nels. (from type tree)

Other material from *B.* x *andrewsii* population from Colorado

B. x *utahensis* Britton (type specimen)

B. *subcordata* Rydb. (type specimen)

B. *montanensis* Butler (type specimen)


Frequency
1
2
3
4
5
6
7
8
9
10
11
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Betula fontinalis
Betula papyrifera
Hybrid index values

of lateral leaf veins. Each individual was plotted (Figure 25).

Stomata and Pollen Grain Morphology

In the Thunder Hill population there were not enough of the parental forms to make an analysis of variance in stomatal size. A summary of stomatal size data is in Table 19.

TABLE 19.

Size of stomata (μ) in Thunder Hill birches.

Taxon	N	Range	Mean	S.D.
B. fontinalis	2	20.2-21.8	21.0	-
B. papyrifera	2	24.3-25.2	24.8	-
B. x *utahensis*	28	18.7-27.3	23.0	2.26

A correlation coefficient was determined comparing the stomatal size of each individual in the population to the hybrid index. The correlation was 0.340 which was not significant at the 5 per cent level.

Clausen (1962) has suggested that the presence of more than three pores in birch pollen may be an indicator of hybrid origin. At Thunder Hill, *Betula fontinalis* has 11 per cent of the grains with less than three pores, and none were found with more than three pores. A single specimen of *B. papyrifera* with mature pollen has 27.9 per cent of the grains with less than three pores and 4.6 per cent with more than three pores. *B.* x *utahensis* has 13.3 per

FIGURE 25.

Pictorial scatter diagram of _Betula_ _fontinalis_, _B_. _papyrifera_, and hybrids.

Key

Bark _color_

Brown

Golden brown

Beige-silver, white

Leaf _length_

Less than 4 cm

4-5 cm

5.1 - 6 cm

More than 6 cm

Exfoliation

Not exfoliating

Partly exfoliating

Exfoliating

Petiole _length_

Less than 1.1 cm

1.1-1.5 cm

1.6-2 cm

More than 2 cm

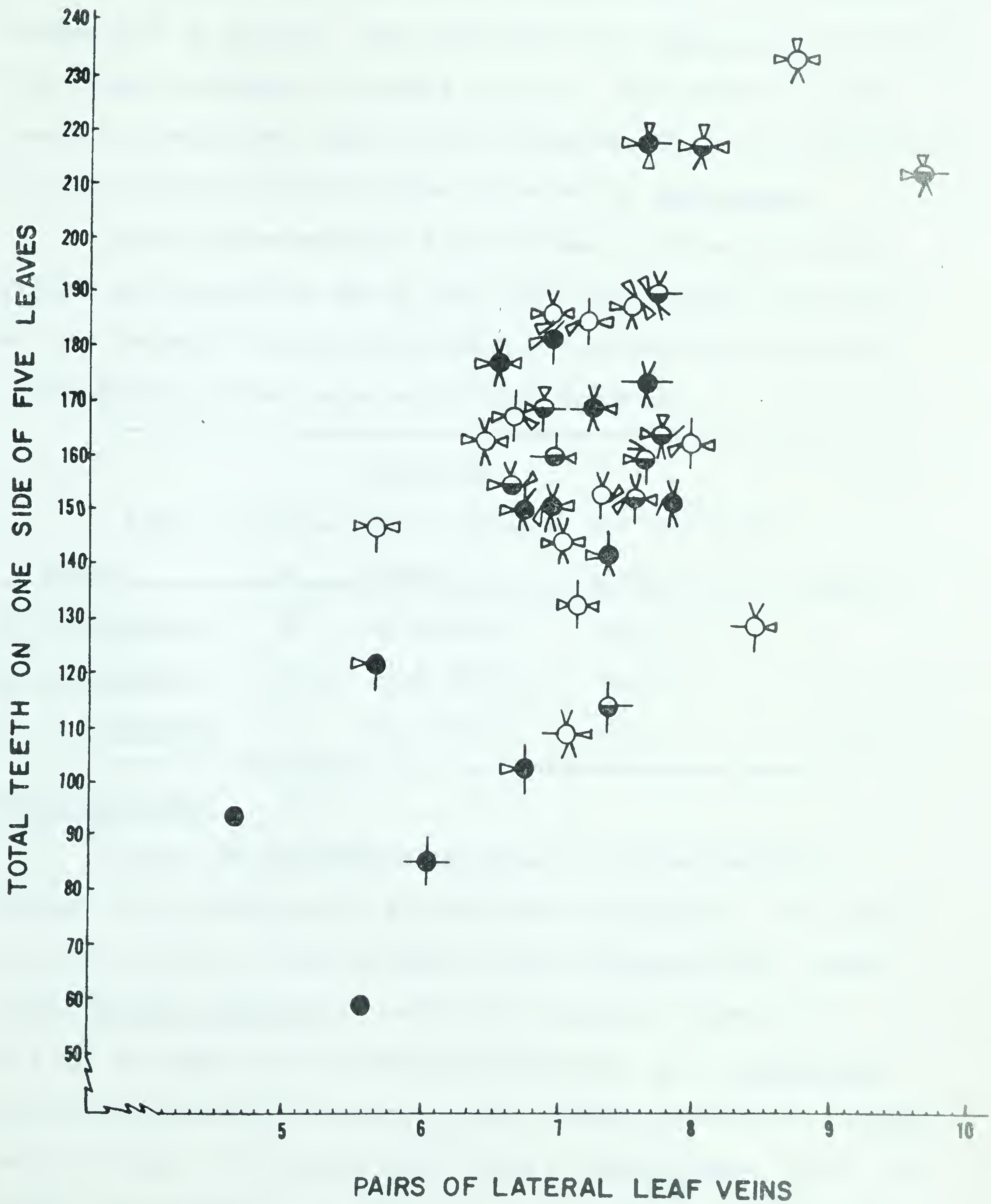
Margin _of_ _leaf_

Serrate

Partly doubly-serrate

Doubly-serrate

Note: When necessary to avoid overlapping, appendages are bent.



TOTAL TEETH ON ONE SIDE OF FIVE LEAVES
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
5
6
7
8
9
10
PAIRS OF LATERAL LEAF VEINS

cent of the grains with less than three pores and 1.8 per cent of the grains with more than three pores. If Clausen's suggestion is correct, the specimen of B. papyrifera analyzed here shows evidence of hybrid nature, even though on the basis of characters used in the analysis, this birch was within the arbitrary hybrid index range of B. papyrifera.

Since there were so few of these birches for which pollen was available and so few that were within the range of the parental taxa, no analysis of variance was applied. A summary of pollen size data is in Table 20 .

TABLE 20 .

Size of pollen (μ) in Thunder Hill birches.

Taxon	N	Range	Mean	S.D.
B. fontinalis	2	24.8-25.6	25.2	-
B. papyrifera	1	25.0-28.2	26.0	-
B. x utahensis	6	24.7-27.3	26.4	1.24

Chromatography

Figure 26 represents tracings of chromatograms of leaves of the Thunder Hill population of birches. Only one of the parents is represented in the chromatograms, number 2338, Betula papyrifera, which has a hybrid index of 23. All of the rest may be considered hybrids, B. x utahensis, arranged according to hybrid index, lowest on left to highest on the right. It may be noted that B. papyrifera, 2338, and number 2339 which has a hybrid index of 20 are missing the

FIGURE 26.

Chromatograms of Betula fontinalis, B. papyrifera and hybrid leaves arranged in order of hybrid index. Each is marked with the collection number.

Key

Bright blue

Light purple

Purple

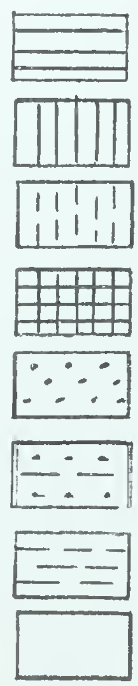
Dark red-purple

Yellow

Orange

Red

Bright yellow in ammonia vapor



The spot at Rf 0.93 in each chromatogram is orange-red.

2326
2321
2332
2336
2329
2330
2331
2337
2333
2335
2328
2334
2339
2338
20
30
40
50
60
70
80
90
100
R_f

yellow spot which is present in all of the other chromatograms at Rf 0.27. The spots which may be correlated with _B. papyrifera_ are a light purple spot at Rf 0.50 and a purple spot at Rf 0.73. It is also interesting to note that there is no bright yellow ammonia vapor spot at Rf 0.67 in _B. papyrifera_. It also can be noted that numbers 2326, 2327, and 2332 which have hybrid indices of 9 and 10 have a greater number and also a greater variety of spots than do the other hybrids or _B. papyrifera_. From these results it was predicted that _B. fontinalis_ in the population perhaps has the following spots: one or two yellow spots at Rf 0.30, two bright blue spots at Rf 0.50 and 0.60 separated by a yellow spot and a light purple spot at Rf 0.70.

An additional set of chromatograms were run to test the above prediction. Several of the same collections were repeated and two collections of _B. fontinalis_ from Thunder Hill were also run. It was found that the greatest difficulty is the difference in qualitative judgements in comparing the spots with previously analyzed chromatograms. The Rf values for the spots were very comparable, but the judgement of color, particularly on blue and purple spots differed. It was found that _B. fontinalis_ had the following spots: all the same as predicted except for the expected bright purple spot at Rf 0.70 which was instead, bright blue.

Chromosome Numbers

The chromosome number of _Betula fontinalis_ is 2n = 28 (Plate 27, Figure 1). Chromosome numbers of _B. papyrifera_

PLATE 27.

Chromosome numbers in *Betula fontinalis*, *B. papyrifera*, and *B.* x *utahensis*.

Fig. 1. *Betula fontinalis*, 2n - 28

Fig. 2. *Betula* x *utahensis*, 2n - 62

Fig. 3. *Betula papyrifera*, 2n - 84

1

2

3

and its varieties have been reported as 2n = 56, 70, and 84 (Woodworth, 1931). Woodworth reported a number of 2n = 56 for B. subcordata, shown above as a later synonym for B. x utahensis. However, no herbarium specimens are available of the material of B. subcordata he counted and so this count is uncertain. Johnsson (1949) and Brittain (1963, 1964, letters) have reported that 2n = 84 is the most common number in western North American B. papyrifera, and this has also been the experience of the writer (Plate 27, Figure 3). Chromosome counts of B. x utahensis collected at Thunder Hill are as follows:

2291. B. x utahensis 2n - c 59*

2293. B. x utahensis 2n - c 62*

(See Plate 27, Figure 2)

2293a. B. x utahensis 2n - c 59*

* These counts are from germinating seed of these hybrid birches, and therefore may or may not be the chromosome numbers for the particular numbered birches.

The chromosome numbers of B. x utahensis are between the numbers of the parental species.

Discussion

It has been shown that at Thunder Hill, B. C., there are two species, Betula fontinalis with 28 chromosomes, and B. papyrifera with 84 chromosomes, which hybridize to form B. x utahensis which usually has an

intermediate number of chromosomes. The variation in the hybrids can be seen in the leaf tracings, polygonal graphs and hybrid index histogram.

Froiland (1952) analyzed a population in Colorado of _Betula fontinalis_ hybridizing with _B. papyrifera_. The chromosome number of the parental _B. papyrifera_ was not determined. Clausen has suggested 2n = 70 or 84 for this _B. papyrifera_, and from the reported frequency of these numbers (Johnsson, 1949; Brittain, 1963, 1964, in letters) and from this investigation, it seems likely to be 2n = 84, since this number occurs more frequently. Froiland found that _B. papyrifera_ had been introgressed by _B. fontinalis_ and the resulting hybrid complex was given formal taxonomic recognition as _B._ x _andrewsii_. As has been shown above, this is a later synonym for _B._ x _utahensis_. When the specimens from Colorado were analyzed together with those from Thunder Hill (pages 188 and 287), it was found that a similar pattern existed in both populations. Froiland suggested that "pure" _B. papyrifera_ was almost absent from the population in Colorado since it had been introgressed by _B. fontinalis_ to such a large extent. Very few of the birches in Thunder Hill fit within the arbitrary range of _B. papyrifera_, and the peak in the frequency of the hybrid population is closest to _B. papyrifera_. A gap can also be seen in the hybrid index histogram between _B. fontinalis_ and the hybrids.

Another feature of importance in the Thunder Hill population is the disturbance of the habitat by the actions of both man and animals. The area has been greatly disturbed by grazing cattle, and in addition it is a campsite and has been partially cleared. As a consequence intermediate habitats have almost certainly been formed.

There is much evidence of variation in the hybrid population as well as in the introgressed *B. papyrifera*. The lack of correlation between the hybrid index and the stomatal size shows the discordance of the population and therefore the fact that introgression has been extreme (Anderson, 1951). The stomatal length of *B. fontinalis* which was found in the population is as expected, but the size of stomata of those birches found within the range of *B. papyrifera* is smaller than expected: Thunder Hill *B. papyrifera*, mean = 24.8μ (collodion); *B. papyrifera*, mean = 28.7 μ (collodion). This difference of 4 μ in *B. papyrifera* shows introgression of *B. papyrifera* by *B. fontinalis*. Using Clausen's suggestion that pore number of an individual pollen grain may be a hybrid indicator, the hybrid nature of *B.* x *utahensis* and *B. papyrifera* in the population is shown by the percentage of individual pollen grains having more or less than the usual three pores. *B. fontinalis* has a higher percentage of regular pollen grains than do *B.* x *utahensis* or *B. papyrifera*.

A sample population of birches was collected at

Celestine Lake in Jasper National Park and was also suspected of being Betula papyrifera introgressed by B. fontinalis. The hybrid indices using the same criteria as were used in the Thunder Hill birches were applied to this population also (Table a7 and a8, and Figure 24). Five were within the arbitrary range of B. fontinalis and two were within the range of B. papyrifera. The remaining thirteen specimens had hybrid indices ranging from 12 to 20. Thus the gap between B. fontinalis and the hybrids is very evident, since there were no birches in the Celestine Lake population which had hybrid indices of 5 through 11. This is evidence of one-way gene flow from B. fontinalis into B. papyrifera, and apparently all of the B. papyrifera has been somewhat affected by it since there were no B. papyrifera with hybrid indices of 23, 24, or 25. Another interesting morphological feature of the introgressed B. papyrifera is the tendency for them to have more than one trunk. This characteristic was also noticed by Froiland (1952) who used it in his hybrid index. In number of trunks, stomatal size, and the characters used in the hybrid index, the variation of characters does not seem to be correlated, which indicates that introgression has taken place. The data available on the Celestine Lake birches are summarized in Table a8.

In both the Thunder Hill and Celestine Lake populations, introgression is from the birch of lower ploidy,

Betula fontinalis (2n = 28), into the birch of higher ploidy, B. papyrifera (2n = 84).

BETULA PAPYRIFERA X BETULA x SARGENTII (B. x arbuscula)

In three areas in western Alberta, Pocahontas, Miette Hot Springs, and Maligne Lake in Jasper National Park, some peculiar birches which resembled *Betula* x *sandbergii* (Plate 28) were found. Collections of these birches and others in the area were made and the total collections, consisting of 33 individuals (hybrids, *B.* x *sargentii*, and *B. papyrifera*) were pooled and analyzed as a single population.

Characters of Gross Morphology Used in the Analysis

A summary of the characters used in the analysis is in Table 21.

Certain intermediate characters were also noted. These are enumerated in Table a9 and the key to Figure a33. Variation in the leaves of this population is illustrated in Figure a32.

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the characters on each of the eight radii of the graphs are shown in Figure a33. A selected group of representative polygons is shown in Figure a34.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table a9.

PLATE 28

Betula x arbuscula (B. x sargentii x B. papyrifera), 1734, 2240. Note the B. papyrifera on the far left of the photograph.

TABLE 21.

Gross morphological characters of _B_. x _sargentii_ and _B_. _papyrifera_ used in the analysis.

Betula x _sargentii_	_Betula papyrifera_
Bark brown	Bark light
Bark non-exfoliating	Bark exfoliating
Branchlets with scattered glands	Branchlets usually without glands
Leaves elliptic	Leaves broadly ovate
Leaf margin crenate-serrate	Leaf margin doubly-serrate
Leaf apex round	Leaf apex abruptly acuminate
Leaf not pubescent	Leaf pubescent in axils of veins
Leaf not lobed	Leaf lobed
Leaf less than 4 cm long	Leaf more than 5 cm long
Leaf less than 3 cm wide	Leaf more than 4 cm wide
Leaf with 10-15 serrations on one margin	Leaf with 30-40 serrations on one margin

In each the index value of 0 is typical of one extreme in the character, and the index value of 2, 3, or 4 is typical of the other extreme. Variation from these extremes is indicated by the intermediate values. A typical _Betula_ x _sargentii_ index ranges from 0-4 and a typical _B_. _papyrifera_ index ranges from 22-26. A list of the hybrid index values of the birches used in the analysis is in Table a10.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of five leaves and the number of pairs of lateral leaf veins. Each individual was plotted (Figure 29).

Germination Data

Germination tests were made of the fruits of *Betula* x *sargentii*, *B.* *papyrifera*, and *B.* x *arbuscula* without prior examination to see if they contained seed. There appears to be evidence of increased germination among these hybrid birches. The results are in Table 22.

TABLE 22.

Percentage germination of the fruits of *Betula* x *sargentii*, *B.* *papyrifera*, and *B.* x *arbuscula*.

Taxon	Hybrid indices	Number of individuals	Number of fruits planted	Percentage germination
B. x *sargentii*	0 - 4	6	200	15%
B. *papyrifera*	20 - 25	3	75	24%
B. x *arbuscula*	5 - 19	3	99	52%

Stomata and Pollen Grain Morphology

The distribution of mean stomatal lengths of the three taxa is presented in Table all. A summary of stomatal size data is in Table 23.

The mean stomatal lengths of *B.* *papyrifera* and *B.* x *arbuscula* are approximately 10 μ greater than that of *B.* x

FIGURE 29.

Pictorial scatter diagram of <u>Betula</u> x <u>sargentii</u>, <u>B</u>. <u>papyrifera</u>, and hybrids.

<u>Key</u>

<u>Bark color</u>

Brown and non-exfoliating

Brown to gray and exfoliating

Beige to silver-white and exfoliating

<u>Leaf length (cm)</u>

Less than 3

3 - 4.9

5 - 6

More than 6

<u>Margin of leaf</u>

Crenate-serrate

Serrate

Partly doubly-serrate

Doubly-serrate

<u>Leaf lobing</u>

Not lobed

Slightly lobed

Lobed

<u>Leaf tip</u>

Round-acute

Acute

Acute-acuminate

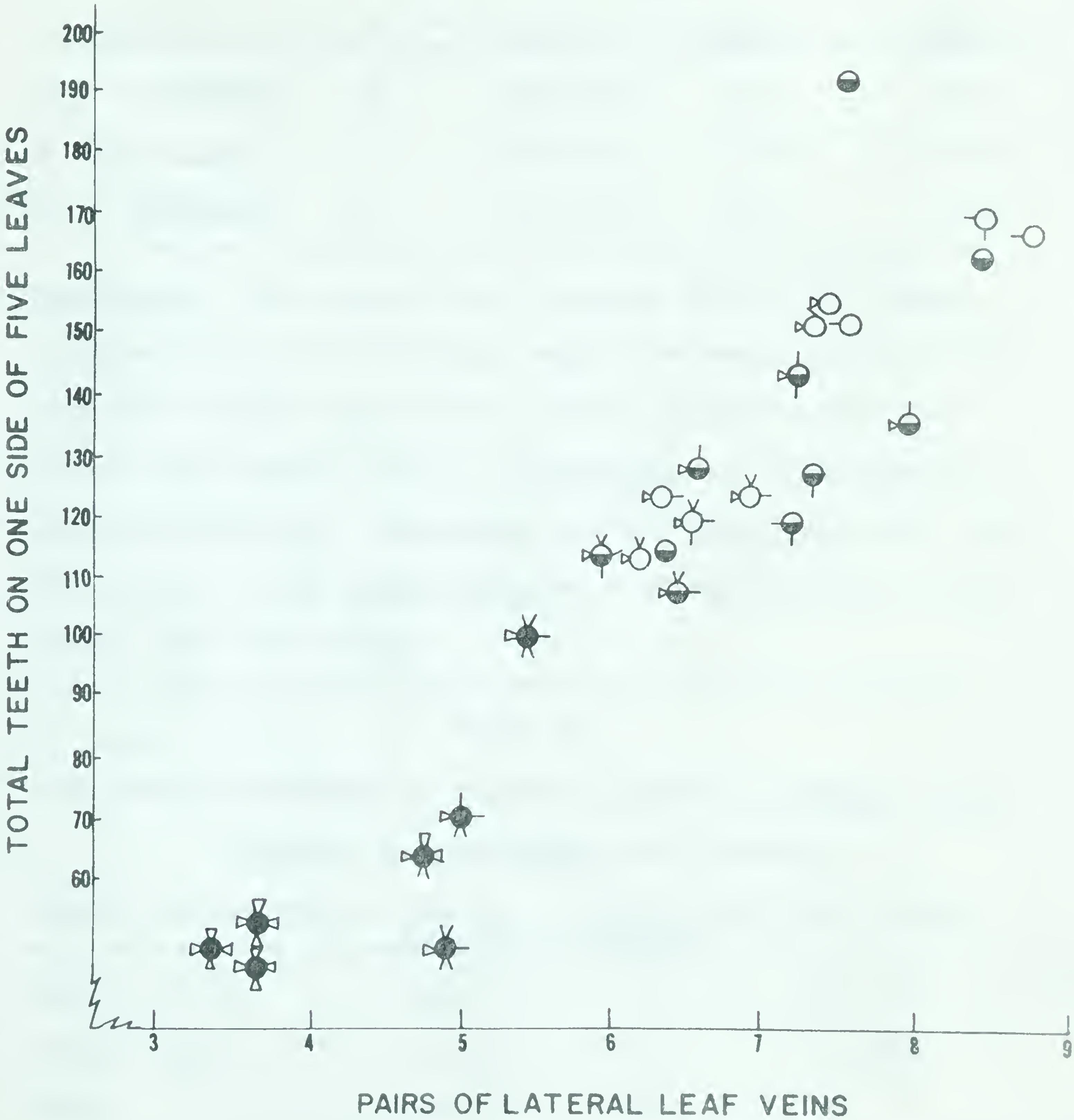

TOTAL TEETH ON ONE SIDE OF FIVE LEAVES
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
3
4
5
6
7
8
9
PAIRS OF LATERAL LEAF VEINS

TABLE 23.

Size of stomata (µ) in _Betula_ x _sargentii_, _B_. _papyrifera_, and _B_. x _arbuscula_.

Taxon	N	Range	Mean	S.D.
_B_. x _sargentii_	8	18.5-24.1	21.1	2.09
_B_. _papyrifera_	6	28.0-34.6	31.9	2.60
_B_. x _arbuscula_	15	23.3-42.0	30.7	4.52

sargentii. The analysis of variance (Table 24) demonstrated that the difference among the means of the three taxa was highly significant and the Duncan's multiple range test showed that _B_. x _sargentii_ was significantly different from _B_. x _arbuscula_ and _B_. _papyrifera_, but that the hybrid and _B_. _papyrifera_ were not significantly different from each other.

TABLE 24.

Analysis of variance in stomatal length in _Betula_ x _sargentii_, _B_. _papyrifera_ and hybrids.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	629.349	2	314.674	23.875**
Within taxa	355.866	27	13.180	
Total	985.215	29		

** Significant at the 1% level.

A summary of pollen size data is in Table 25.

TABLE 25.

Size of pollen (μ) in *Betula* x *sargentii*, *B. papyrifera*, and *B.* x *arbuscula*.

Taxon	N	Range	Mean	S.D.
B. x *sargentii*	5	15.4-22.6	19.9	3.20
B. papyrifera	1	21.0-26.8	23.5	-
B. x *arbuscula*	6	21.0-30.9	25.3	3.29

The samples were not large enough for an analysis of variance to be performed. One can only say that there is a tendency for pollen of *B.* x *arbuscula* and *B. papyrifera* to be larger than that of *B.* x *sargentii*. For comparison of pollen of *B.* x *arbuscula* with that of *B. papyrifera*, see Plate 30, Figures 1 and 2.

Chromosome Numbers

The chromosome number of *Betula* x *sargentii* is 2n = 28 - 56 (Plate 19, Figure 3). Chromosome numbers of 2n = 70 and 84 were obtained from samples of *B. papyrifera* involved in this hybrid population. The number of chromosomes visible at diakinesis is 42 in *B.* x *arbuscula*. It is nearly impossible to distinguish bivalents from univalents. It is thought that other chromosome numbers ranging from 28 to 84 could occur in other individuals of this hybrid taxon. Numbers of birches in this population

PLATE 30

Pollen of Betula.

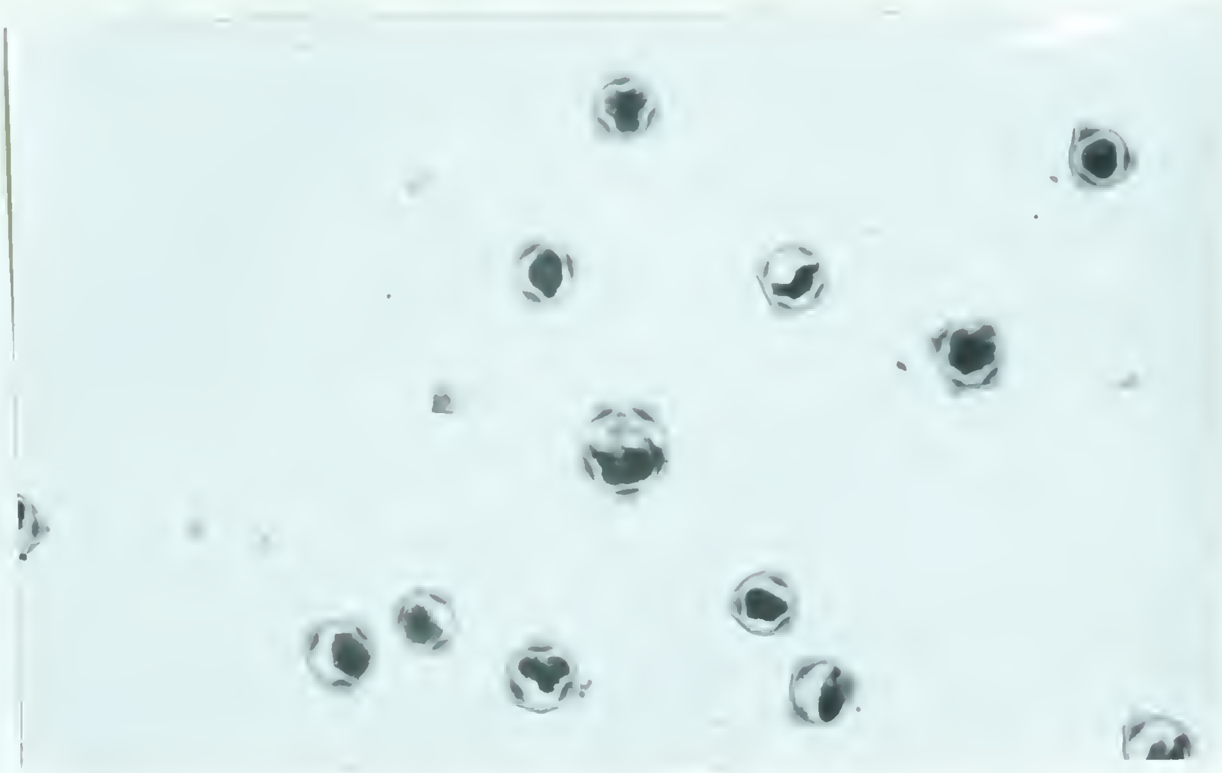


Fig. 1.
Pollen of Betula x arbuscula, 1734, 2240 (x 250). Note several of the pollen grains have more than three pores.

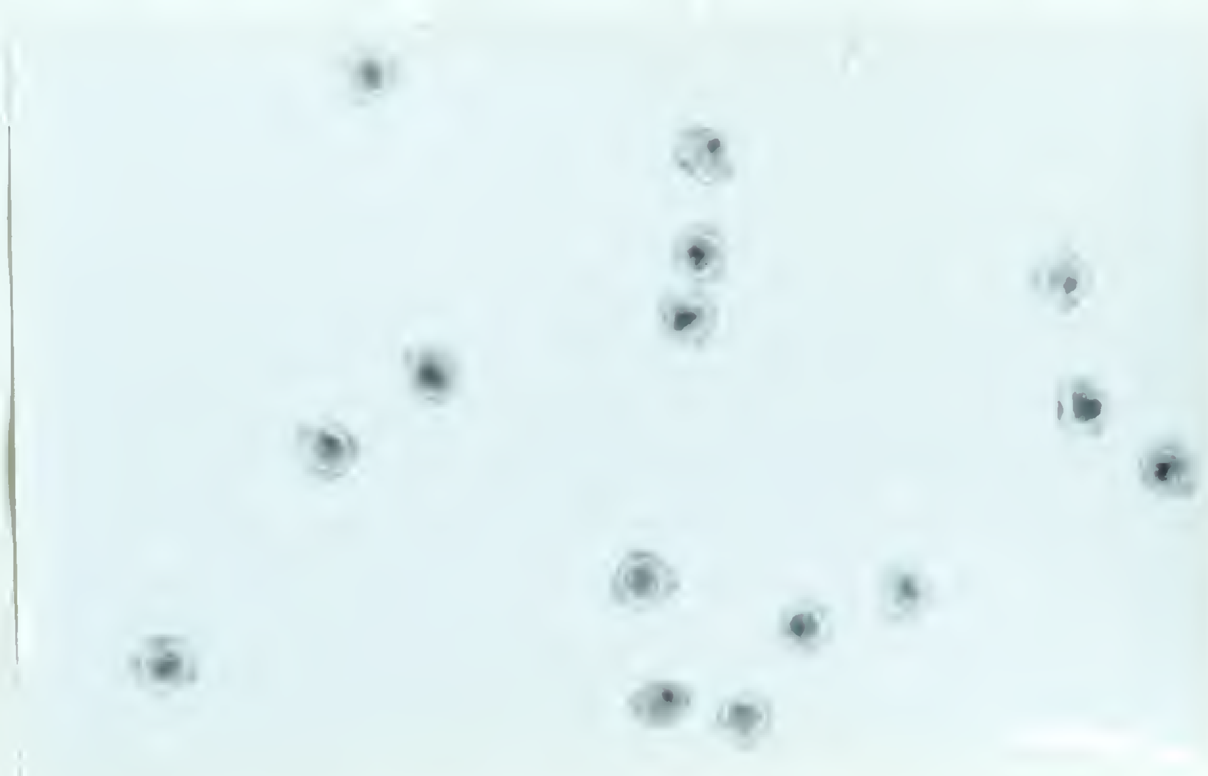


Fig. 2.
Pollen of Betula papyrifera, 1766 (x250). Most of the pollen grains are regularly three pored.

are:

1737. *B. papyrifera* 2n = *c* 70

1738. *B. x arbuscula* 2n = *c* 63*

*This count is from germinating seed of this hybrid birch, and therefore may or may not be the chromosome number for the particular numbered birch.

Discussion

This sample was a very small one, and so the conclusions here presented are tentative. Examination of the scatter diagram and polygonal graphs suggests that *B. papyrifera* has been influenced by genes from *B. x sargentii*. In this population the birch of higher ploidy is introgressed by the birch of lower ploidy. It is interesting to note that the habitat has been influenced by man in at least two of the areas where the hybrid appeared, in one case through building a railroad right of way, and in another by construction of trails.

BETULA PAPYRIFERA X *BETULA RESINIFERA* (*B.* x *winteri*)

In various localities near Edmonton in central Alberta, *Betula papyrifera* and *B. resinifera* were found growing together. Certain other individuals that were suspected of being hybrids between the two were also found. Collections were made in these areas, consisting of 97 individuals of *B. papyrifera*, *B. resinifera*, and the hybrids, and the collections were pooled and analyzed as a single population. Certain other comparisons were made of *B. papyrifera* and *B. resinifera* collections from other areas in Alberta.

Characters of Gross Morphology Used in the Analysis

A summary of the characters used in the analysis is in Table 26.

Certain intermediate characters were also noted. These are listed in Table a12 and the key to Figure a36. Variation in the leaves of this population is illustrated in Figure a35.

The Polygonal Graphs

The assigned values of the characters on each of the eight radii of the polygonal graphs are shown in Figure a36. A selected group of representative polygons are shown in Figure a37.

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table a12. For

TABLE 26.

Gross morphological characters of *Betula papyrifera* and *B. resinifera* used in the analysis.

Betula papyrifera	*Betula resinifera*
Branchlets without resinous glands	Branchlets with resinous glands
Leaves broadly ovate to elliptic	Leaves deltate to trullate
Margin doubly-serrate	Margin partly doubly-serrate to doubly-serrate
Apex short acuminate	Apex long acuminate
Leaf pubescent in vein axils below	Leaf glabrous below
Leaf with 30-40 serrations on one margin	Leaf with 20-30 serrations on one margin
Leaf with more than 8 pairs of lateral leaf veins	Leaf with less than 7 pairs of lateral leaf veins
Leaf more than 6 cm long	Leaf less than 5 cm long

each character, the index value of 0 is typical of one extreme in the character, and the index values of 1, 2, 3, or 4 are typical of the other extreme. Variation from these extremes is indicated by the intermediate values. *B. resinifera* typically has an index value ranging from 0-3 and the limits set for a typical *B. papyrifera* index range from 17-20.

The total index value for each tree was determined from the individual sets of measurements, and a bar graph was constructed upon which the hybrid index values were

plotted against their frequencies (Figure 31).

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of one leaf and the number of pairs of lateral leaf veins. Each individual was plotted (Figure 32).

Germination Data

Germination tests were made of the fruits of *Betula resinifera*, *B. papyrifera* and *B. x winteri*. The fruits were tested without prior examination to see if they contained seed. There is some evidence of reduction in fertility in the hybrids. The results are in Table 27.

TABLE 27.

Percentage germination of the fruits of *Betula resinifera*, *B. papyrifera* and *B. x winteri*.

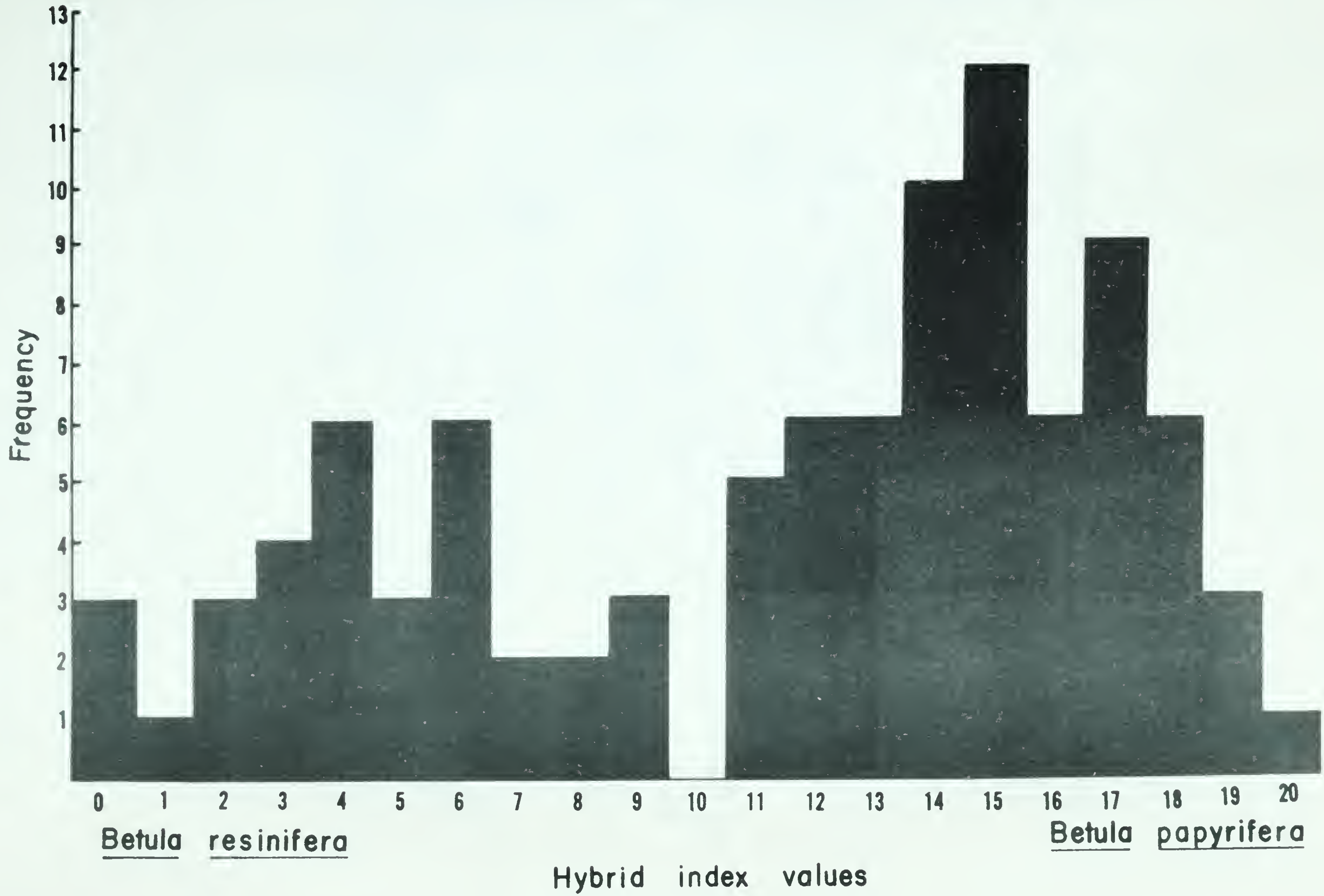
Taxon	Hybrid indices	Number of individuals	Number of fruits planted	Percentage germination
B. resinifera	0 - 4	8	225	40%
B. papyrifera	16 - 20	14	340	56%
B. x winteri	5 - 15	10	289	29%

Stomata and Pollen Grain Morphology

The distribution of mean stomatal lengths of the two species, *Betula papyrifera* and *B. resinifera*, from many collecting areas in Alberta is presented in Table 28. A summary of the stomatal length data on these two species from many collection areas in Alberta is presented in Table 29.

FIGURE 31.

Frequency of hybrid index values of *Betula resinifera*, *B. papyrifera*, and hybrids.



Frequency
13
12
11
10
9
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Betula resinifera
Betula papyrifera
Hybrid index values

FIGURE 32.

Pictorial scatter diagram of *Betula resinifera*, *B. papyrifera*, and hybrids

Key

Branchlets

Glandular

Not glandular

Leaf epidermis

Glabrous below

Pubescent in vein axils below

Leaf shape

Widest point below the mid-point

Widest point at the mid-point

Margin

Serrate

Partly doubly-serrate

Doubly-serrate

Pairs of lateral leaf veins

6

7

8

Note: If necessary to avoid overlapping, appendages are bent.

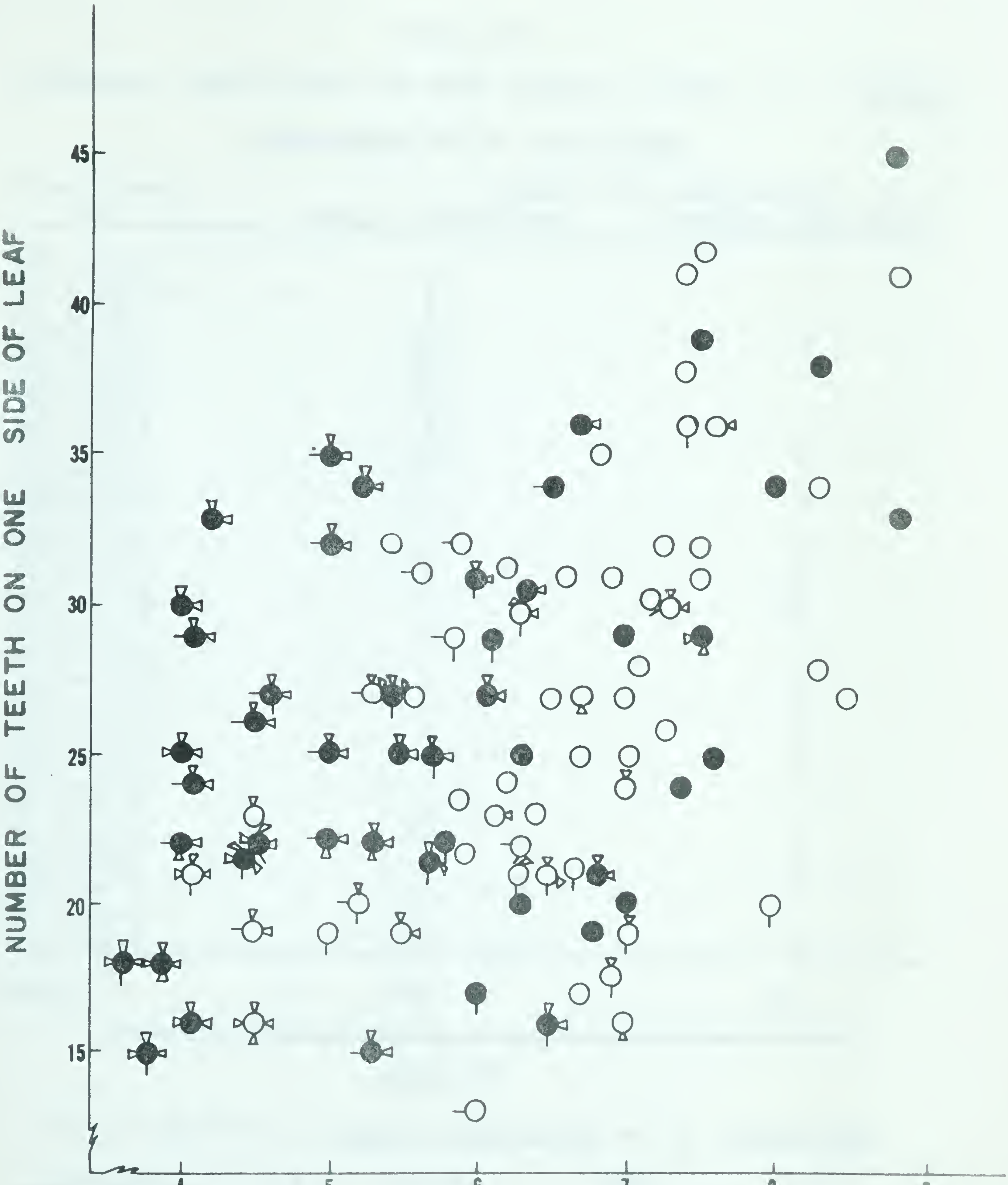

NUMBER OF TEETH ON ONE SIDE OF LEAF
45
40
35
30
25
20
15
4
5
6
7
8
9
LEAF LENGTH (CM)

TABLE 28.

Frequency distribution of mean stomatal length (μ) in *Betula resinifera* and *B. papyrifera*.

Size class (μ)	Number of Individuals Betula resinifera	Betula papyrifera
15.1-16.0	1	-
16.1-17.0	1	-
17.1-18.0	1	-
18.1-19.0	11	1
19.1-20.0	17	-
20.1-21.0	11	-
21.1-22.0	9	2
22.1-23.0	18	4
23.1-24.0	13	5
24.1-25.0	11	9
25.1-26.0	-	8
26.1-27.0	3	9
27.1-28.0	1	19
28.1-29.0	-	11
29.1-30.0	-	9
30.1-31.0	-	7
31.1-32.0	-	8
32.1-33.0	-	8
33.1-34.0	-	4
34.1-35.0	-	5
35.1-36.0	-	3
36.1-37.0	-	-
37.1-38.0	-	1
38.1-39.0	-	2
39.1-40.0	-	-
40.1-41.1	-	-
41.1-42.0	-	1
Total	97	116

TABLE 29.

Size of stomata in *Betula papyrifera* and *B. resinifera*

Species	N	Range	Mean	S.D.
B. resinifera	97	15.6-27.8	21.6	2.41
B. papyrifera	116	18.6-42.0	28.7	4.08

The mean stomatal length of B. resinifera was therefore about 7 μ smaller than that of B. papyrifera.

A t test for unpaired data was applied to the stomatal size of the two species, Betula resinifera and B. papyrifera. Measurements were made on 97 B. resinifera leaves and 116 B. papyrifera leaves, each from a different tree. The standard error of the mean difference was 0.4508, and t = 15.809, significant at the 1 per cent level.

When Betula papyrifera is in contact with B. resinifera, hybrids are formed. The populations from near Edmonton where both species and hybrids are growing together were analyzed separately. The distribution of mean stomatal lengths in these populations are in Table a13. In these populations the means and standard deviates differed. A summary of these data is in Table 30.

TABLE 30.

Size of stomata (μ) in Betula papyrifera, B. resinifera and B. x winteri

Taxon	N	Range	Mean	S.D.
B. resinifera	6	15.6-23.3	20.0	2.92
B. papyrifera	20	21.7-38.6	27.3	4.42
B. x winteri	33	18.6-37.7	27.3	4.36

The analysis of variance (Table 31) demonstrated that the difference between the means of the three taxa was highly significant and the Duncan's multiple range test

showed that B. resinifera was significantly different from B. x winteri and B. papyrifera, but that the latter two taxa were not significantly different from each other.

TABLE 31.

Analysis of variance in stomatal length in Betula resinifera, B. papyrifera and hybrids.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	286.40	2	143.20	7.834**
Within taxa	1023.49	56	18.28	
Total	1309.89	58		

** significant at the 1% level.

The pollen of Betula resinifera ranges from 17.2 µ to 24.2 µ with a mean of 20.9 µ and a standard deviation of 2.47. B. papyrifera pollen ranges from 23.5 µ to 26.1 µ with a mean of 25.2 µ in a sample too small for analysis. The B. papyrifera pollen is smaller than reported by Clausen (1962), 28.2 µ or by Cain (1953), 27.8 µ and 37.0 µ.

Chromosome Numbers

The chromosome number of Betula resinifera is 2n = 28 (Plate 33, Fig. 3 and 4). Chromosome numbers of B. papyrifera are 2n = 56-84 (Plate 33, Fig. 1 and 2). The chromosome number of the hybrid birch was found to be 2n = 28-84 with a concentration of individuals at 2n = 56. The individual collections for which chromosome numbers have been determined are listed in Table a14.

PLATE 33

Chromosome numbers in _Betula resinifera_ and _B. papyrifera_.

Fig. 1. _Betula papyrifera_, n = 42

Fig. 2. Drawing of same cell, _Betula papyrifera_.

Fig. 3. _Betula resinifera_, n = 14

Fig. 4. Drawing of same cell, _Betula resinifera_.

1

2

3

4

Discussion

In the hybrid, *Betula* x *winteri*, there is a concentration of chromosome numbers at 2n = 56. This may indicate an origin for some of the 56 chromosome birches found in western Canada, in addition to their origin from crosses between *B. papyrifera* and *B. fontinalis* discussed on page 103.

From an examination of the hybrid index histogram, there appear to be two peaks present, one beginning in the range of *Betula resinifera*, and the other beginning within the range of *B. papyrifera*, but both extending into the intermediate region. It seems that introgression has proceeded in both directions, and that genes from each birch are causing variation in the other. These birches were found in environments which had been disturbed by human activity. The forested area, particularly along river bluffs, is best suited to *B. papyrifera*. However, in areas which have been disturbed, the hybrids are more successful. *B. resinifera* is less commonly found in the forested environment.

Therefore there are at least two factors present influencing the direction of introgression. Clausen (1962) has suggested that gene flow is in the direction of higher ploidy, that is from *Betula resinifera* to *B. papyrifera*. So far in this thesis, this has been shown to be true. However, in the case of *B.* x *winteri*, another factor is

influencing introgression, the environment. Thus there is also a tendency for gene flow to be in the direction of *B. resinifera*, modifying these birches for better adaptation to the forested environment.

BETULA PAPYRIFERA X *BETULA PUMILA* VAR. *GLANDULIFERA* (*B. x sandbergii*)

In two localities disturbed by human activity, White Mud Creek, a municipal park area in Edmonton, and in Elk Island National Park, Alberta, *Betula papyrifera* and *B. pumila* var. *glandulifera* come in contact, and the hybrid between them, *B. x sandbergii*, is found. This is a very characteristic hybrid, having been first determined as such by Rosendahl (1916). Collections from these two localities, consisting of 77 individuals, were pooled and analyzed as a single population.

Characters of Gross Morphology Used in the Analysis

A summary of the characters used in the analysis is in Table 32.

Certain intermediate characters were also noted. These are listed in Table a15 and the key to Figure a39. Variation in the leaves of these populations can be seen in Figure a38.

The Polygonal Graphs

Polygonal graphs were constructed for each plant analyzed. The assigned values of the characters on each of the eight radii of the graphs are shown in Figure a39. A selected group of representative polygons are illustrated in Figure a40.

TABLE 32.

Gross morphological characters of *Betula papyrifera* and *B. pumila* var. *glandulifera* used in the analysis.

Betula papyrifera	*Betula pumila* var. *glandulifera*
Bark exfoliating	Bark non-exfoliating
Bark light	Bark brown
Branchlets not glandular	Branchlets glandular
Leaves broadly ovate	Leaves obovate
Leaf tip short-acuminate	Leaf tip round
Leaf margin doubly-serrate	Leaf margin crenate
Leaf pubescent in vein axils below	Leaf glabrous below
Leaf more than 6 cm long	Leaf less than 3 cm long
Leaf with 30-40 serrations on one margin	Leaf with 10-15 serrations on one margin
Leaf with more than 8 pairs of lateral leaf veins	Leaf with less than 5 pairs of lateral leaf veins

The Hybrid Index

The characters used in this analysis and the hybrid index values assigned to them are listed in Table al5. For each character the index value of 0 is typical of one extreme in the character and the index value of 1, 2, 3, or 4 is typical of the other extreme. An arbitrary range of 0-3 was selected for *B. pumila* var. *glandulifera*, and a range of 20-23 was selected for *B. papyrifera*.

The total index value for each birch was determined from the individual sets of measurements, and a bar graph

was constructed upon which the hybrid index values were plotted against their frequencies (Figure 34). The hybrid index value of the type specimen of *Betula sandbergii* was also determined and this individual was also plotted.

Pictorialized Scatter Diagram

The characters used as coordinates were number of teeth on one side of one leaf and the number of pairs of lateral leaf veins. Data for each individual were plotted (Figure 35).

Germination Data

Germination tests were made of the fruits of *Betula pumila* var. *glandulifera*, *B. papyrifera*, and *B.* x *sandbergii* without prior examination to see if they contained seed. The results are in Table 33.

TABLE 33.

Percentage germination of the fruits of *Betula pumila* var. *glandulifera*, *B. papyrifera* and *B.* x *sandbergii*.

Taxon	Hybrid indices	Number of individuals	Number of fruits planted	% germination
B. pumila var. *glandulifera*	0 - 4	6	133	0
B. papyrifera	19 - 23	5	126	6
B. x *sandbergii*	5 - 18	3	75	7

Size of Stomata

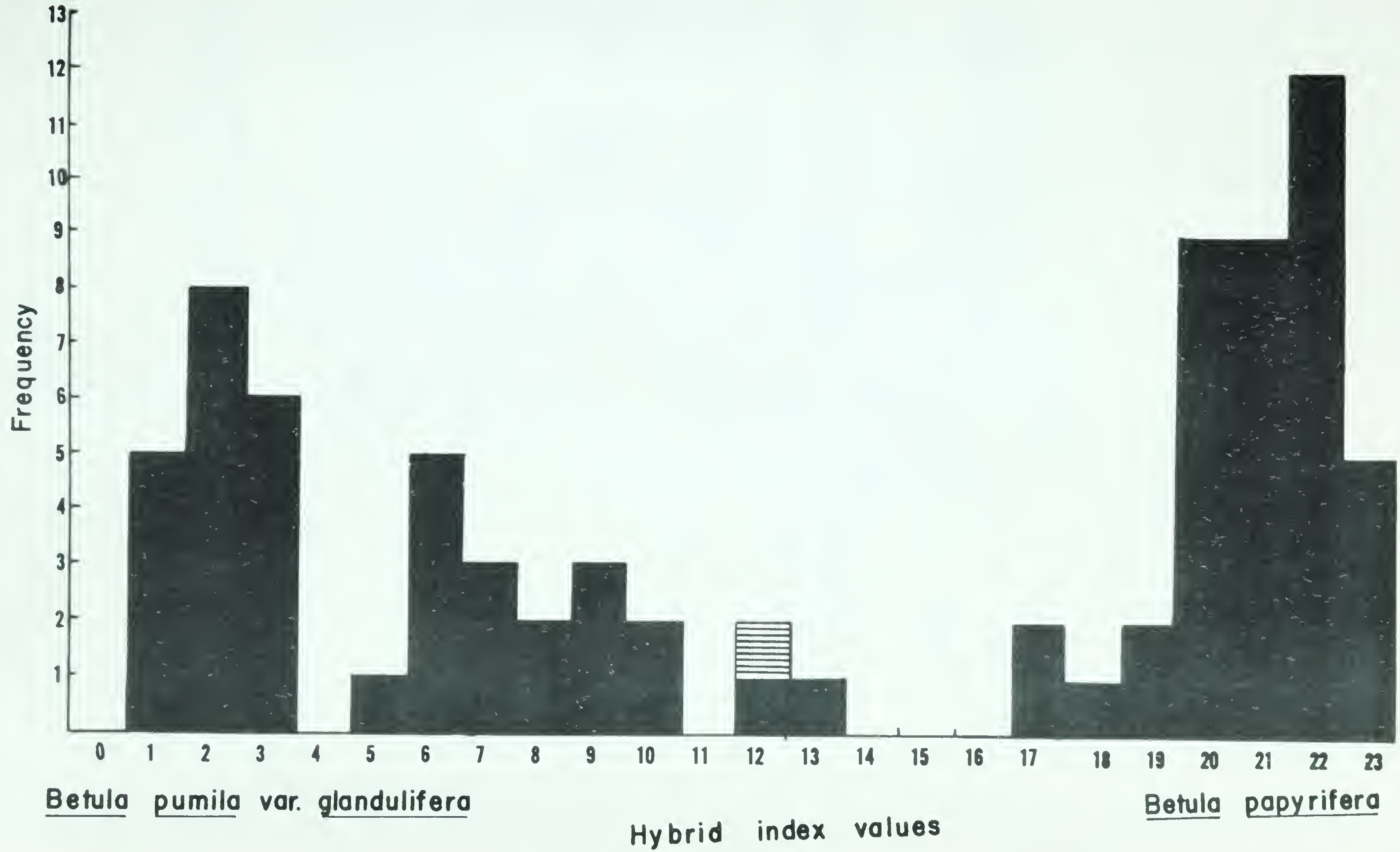
The distribution of mean stomatal lengths of the three

FIGURE 34.

Frequency of hybrid index values of *Betula pumila* var. *glandulifera*, *B. papyrifera*, and hybrids.

Key

June, 1890, J. H. Sandberg, type of *Betula sandbergii* Rosendahl.



Frequency
13
12
11
10
9
8
7
6
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Betula pumila var. glandulifera
Betula papyrifera
Hybrid index values

FIGURE 35.

Pictorial scatter diagram of _Betula pumila_ var. _glandulifera_, _B. papyrifera_, and hybrids.

Key

Bark color and exfoliation

Brown and non-exfoliating

Dark and exfoliating

Light and exfoliating

Margin

Crenate

Crenate-serrate

Serrate and partly doubly-serrate

Doubly-serrate

Branchlet glands and leaf pubescence

Glandular; not pubescent

Glandular; pubescent

Not glandular; not pubescent

Not glandular; pubescent

Pairs of lateral leaf veins

4

5

6

7 or more

Leaf tip

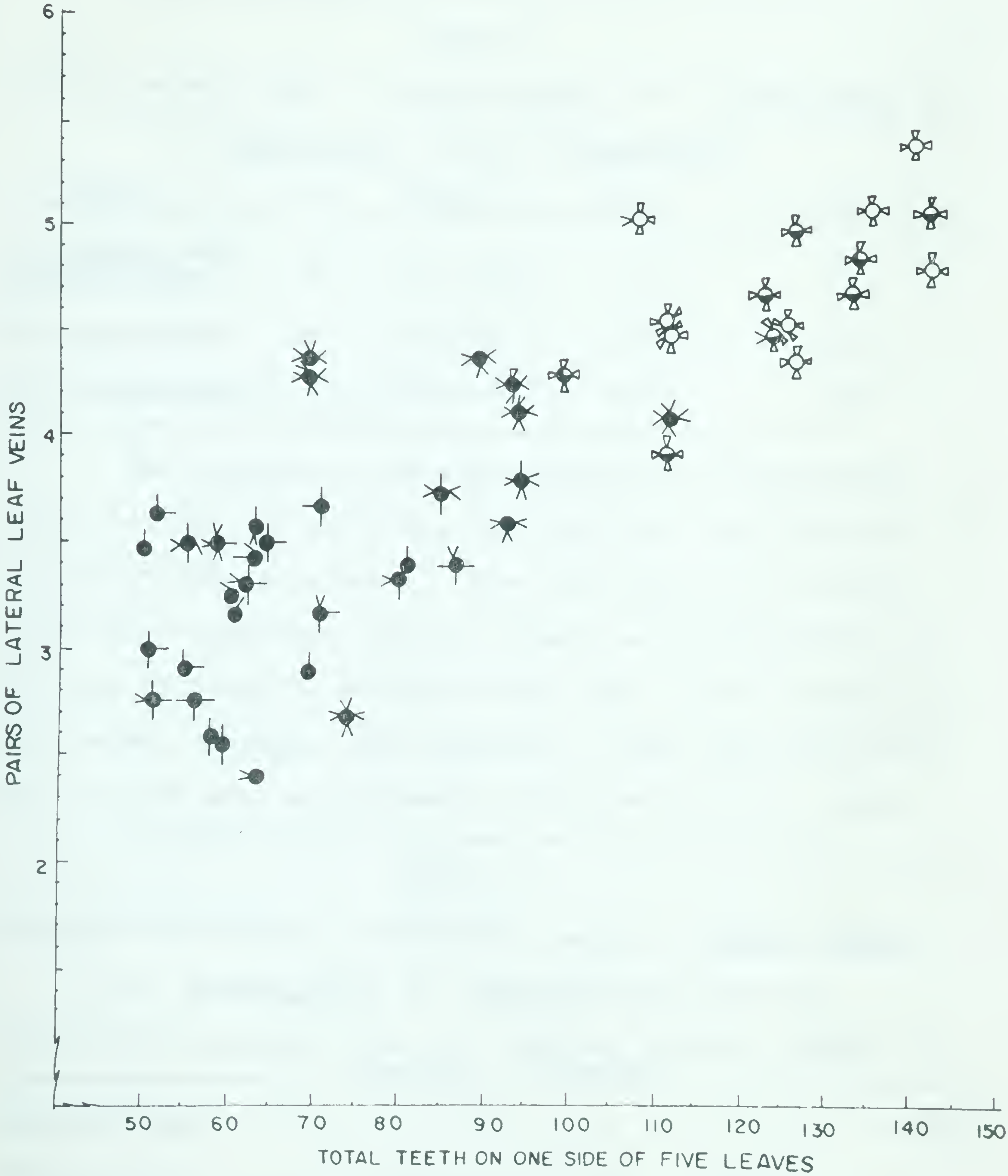
Round

Round-acute

Acute

Acuminate

Note: If necessary to avoid overlapping, appendages are bent.



6
5
4
3
2
PAIRS OF LATERAL LEAF VEINS
50
60
70
80
90
100
110
120
130
140
150
TOTAL TEETH ON ONE SIDE OF FIVE LEAVES

taxa is presented in Table a16. A summary of stomatal size data is in Table 34 .

TABLE 34 .

Size of stomata (μ) in _Betula_ _pumila_ var. _glandulifera_, _B_. _papyrifera_, and _B_. x _sandbergii_.

Taxon	N	Range	Mean	S.D.
_B_. _pumila_ var. _glandulifera_	9	22.7-29.7	25.3	3.74
_B_. _papyrifera_	17	21.8-37.7	28.6	4.21
_B_. x _sandbergii_	7	21.7-33.7	26.7	3.59

The analysis of variance (Table 35) demonstrated that the means of the three taxa were not significantly different from each other. When the means are not significantly different, that is, there is no significant F, the use of Duncan's Multiple range test is not necessarily warranted. However, when applied, it was found that none of the taxa were significantly different from any other.

TABLE 35.

Analysis of variance in stomatal length in _Betula_ _pumila_ var. _glandulifera_, _B_. _papyrifera_ and hybrids.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F
Between taxa	70.37	2	35.2	0.201
Within taxa	5591.70	32	174.7	
Total	5662.10	34		

Chromosome Numbers

The chromosome number of *Betula pumila* var. *glandulifera* is 2n = 56 (Woodworth, 1931) and that of *B. papyrifera* is 2n = 70-84 (Johnsson, 1949). The chromosome number of *B.* x *sandbergii* was found by Woodworth (1931) to be 2n = 63. The only individual of *B.* x *sandbergii* for which accurate chromosome number determination has been made is collection number 2200 for which the number n = 28 was determined in Metaphase I. It is expected that the chromosome number of the hybrid, *B.* x *sandbergii*, varies from 56 - 84.

Discussion

A comparison can be made between the results obtained by Clausen (1963) in Minnesota and those in this study (Table 36). Clausen's measurements were on the basis of five trees for each of the three taxa. In Table 36 the Alberta measurements are corrected for collodion treatment.

TABLE 36.

Comparison of stomatal length (μ) analysis of *Betula pumila* var. *glandulifera*, *B. papyrifera*, and *B.* x *sandbergii* in Minnesota and Alberta.

Taxon	Alberta range	Minnesota range	Alberta mean	Minnesota mean
B. pumila var. *glandulifera*	32.0-39.0	28.1-46.0	34.6	35.9
B. papyrifera	31.1-47.0	31.1-55.0	37.9	39.2
B. x *sandbergii*	31.0-43.0	28.1-55.0	36.0	39.9

It can be seen that the values for the parental taxa are comparable, but the values for *B.* x *sandbergii* differ nearly 4 μ in the mean value. This can be partially explained by a difference in the direction of introgression as indicated below.

This is one of the few cases in which it is possible to compare similar studies of hybrid populations involving the same birch taxa. Clausen (1959, 1962, 1963) has concluded that *B. papyrifera* has been introgressed by *B. pumila* var. *glandulifera*. From an analysis of the hybrid index histogram, the polygonal graphs, and the scatter diagram, it seems likely that in the Alberta population investigated there is some introgression in the direction of *B. papyrifera*. However, a much greater gene flow is in the direction of var. *glandulifera*. The hybrids are closer to var. *glandulifera* and there is a rather large gap evident in the hybrid index histogram between the hybrids and *B. papyrifera*. *B. pumila* var. *glandulifera* also showed considerable variation in morphology which indicates introgression in that direction. These birches were found in open forested areas which are more suitable for a *B. papyrifera* population than for *B. pumila* var. *glandulifera* which requires moist bog conditions. Therefore the situation differed from that found in the Minnesota bogs in which the habitat varied from bog to forest, and could support either parental birch, and hybridization of the

habitat had occurred allowing for survival of the hybrids. In the White Mud Park area the bog habitat was drained leaving only the disturbed habitat suitable for the hybrids and the forested area suitable for *B. papyrifera* survival. *B. pumila* var. *glandulifera* which received genes from the paper birch was better adapted to the hybrid environment available, and *B. papyrifera* birches which received genes from the bog birch were probably subjected to environmental selection, and survival was minimal. In a few more years it is suspected that very few *B. pumila* var. *glandulifera* individuals will remain in the area, and that the only ones which will be able to survive are those with genes from *B. papyrifera*. If both parental birches were not able to survive equally well in the Minnesota populations, a similar pattern would no doubt develop. Therefore, with little or no environmental selection, there is a tendency for introgression to be in the direction of higher ploidy, but when such selection is present, it influences the flow of genes in the direction of the least well adapted birch.

SUMMARY

The genus *Betula* in western Canada has been analyzed using several modern techniques. The analysis was based on over 1000 collections made during 1961-1963 in Alberta and British Columbia, and material from several herbaria.

A new series in the genus *Betula* is described, *Fontinalae*. *Betula fontinalis* has been assigned to this new series.

Five species and seven hybrids are described, four of the latter for the first time. This contrasts with the most recent treatment of western Canadian birches (Moss, 1959) which inculded only four species and no hybrids. To be found with the descriptions of each of the taxa considered is a full synonymy, geographical distribution and cytological data.

The names, chromosome numbers and habitat of the birches studied are as follows:

Betula fontinalis	2n = 28	Foothills, mountains and river valleys in western United States and Canada
Betula glandulosa	2n = 28	Mountain areas of the United States and Canada, and northern Canadian bogs
Betula pumila var. *glandulifera*	2n = 56	Bogs throughout north-western United States and Canada

Betula resinifera	2n = 28	Bogs and sandhills of north-central to northwestern Canada
Betula papyrifera	2n = 56-84	Forests throughout northern United States and Canada
Betula x *uliginosa* (*B. resinifera* x *B. pumila* var. *glandulifera*)	2n = 28-56	Bogs in central Alberta
Betula x *sargentii* (*B. glandulosa* x *B. pumila* var. *glandulifera*)	2n = 28-56	Foothills and mountains of western Canada and northern Canadian bogs
Betula x *eastwoodae* (*B. fontinalis* x *B. glandulosa*)	2n = 28	Foothills and mountains in western Canada and where the parents are in contact in northern Canada
Betula x *utahensis* (*B. papyrifera* x *B. fontinalis*)	2n = 28-84	Foothills and mountains in western Canada and Colorado mountains
Betula x *arbuscula* (*B.* x *sargentii* x *B. papyrifera*)	2n = 28-84	Rare, only in disturbed areas in Alberta Rocky Mountains
Betula x *winteri* (*B. papyrifera* x *B. resinifera*)	2n = 28-84	Areas where the species are in contact in central Alberta
Betula x *sandbergii* (*B. papyrifera* x *B. pumila* var. *glandulifera*)	2n = 56-84	Central Alberta, Saskatchewan, and bogs in North Dakota and Minnesota

A table showing the pattern of natural hybridization among the western Canadian birches is below:

	B. fontinalis	*B. resinifera*	*B. pumila* var. *glandulifera*	*B. glandulosa*	*B.* x *sargentii*
B. papyrifera	X	X	X	0	X
B. fontinalis	-	0	0	X	0
B. resinifera		-	X	0	0
B. pumila var. *glandulifera*			-	X	X
B. glandulosa				-	X

Those combinations which are marked with a 0 were not found in the areas studied. This does not mean that these hybrids do not exist, and in some cases they have been reported. No hybrids of *Betula resinifera* with *B. fontinalis* or *B. pumila* var. *glandulifera* with *B. fontinalis* were found, probably because these species have different ecological and geographical requirements. The same is true of *B. resinifera* and *B. glandulosa*, although these species are in contact in northern Canada, and hybrids between them have been reported. It is possible that *B. glandulosa* and *B. papyrifera* hybrids exist where they are in contact in the Rocky Mountains, but the two species seem to be

ecologically restricted and were not found growing together. B. x sargentii is a hybrid taxon, and therefore hybrids with it are less common. It is not in contact with B. resinifera and no hybrids were found. It is possible that hybrids with B. fontinalis exist, but these would be difficult to distinguish from hybrids of B. fontinalis x B. glandulosa.

Isolating barriers between species within the genus Betula do not seem to be associated with the series boundaries or chromosome number, but seem to be most commonly external: ecological or spatial. When two species are in contact, they may hybridize; and if there is an ecological niche for the offspring, they survive and may, despite a certain amount of hybrid sterility, cross with either of the parents.

Introgressive hybridization was found to be a common phenomenon among the birches studied. A hypothesis proposed by Clausen (1962) that gene flow is in the direction of higher degree of ploidy was found to hold in the cases of Betula x uliginosa, B. x utahensis, and B. x arbuscula. In two hybrids, B. x sargentii and B. x winteri, introgression was in both directions. In B. x winteri populations two factors were operating that affected introgression, preferential environmental selection which favored B. papyrifera (gene flow modified B. resinifera in the direction of B. papyrifera) and also degree of ploidy

which modified _B. papyrifera_ in the direction of _B. resinifera_. In one case, _B. x sandbergii_, introgression was found to be towards the parent with the lower chromosome number. Where the parental species, _B. papyrifera_ and _B. pumila_ var. _glandulifera_, were found in contact in Alberta, the environments preferentially favored _B. papyrifera_. In these habitats, gene flow was in the direction of _B. pumila_ var. _glandulifera_ rather than in the direction of the parent with the higher chromosome number, _B. papyrifera_, as had been reported for Minnesota _B. x sandbergii_ (Clausen, 1962).

There is no special environmental selection operating in the cross of _Betula fontinalis_ and _B. glandulosa_, and the number of _B. x eastwoodae_ individuals in the populations often equals each parent. _B. x eastwoodae_ results from the above cross and does not involve _B. resinifera_ as was previously reported (Hultén, 1944; Krüssmann, 1962).

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APPENDIX

PLATE a1

Photographs of Birch Seedlings

Figure 1. Betula papyrifera (1665)
Stems and petioles commonly pubescent; leaves cordate, large, with pubescent surface; margin of leaves commonly coarsely serrate, rarely to almost crenate.

Figure 2. Betula resinifera (1609)
Stems and petioles commonly glabrous; smaller than B. papyrifera, with pubescent surface; margin of leaves commonly serrate, but finer than B. papyrifera.

Figure 3. Betula fontinalis (1673)
Stems and petioles commonly glabrous but stipules usually pubescent; leaf base varies from truncate to cordate, surface glabrous to sparsely pubescent; margin of leaves serrate to crenate.

Figure 4. Betula x sargentii (1721)
Stems and petioles commonly glabrous; leaf base truncate, leaves glabrous; margin of leaves crenate.

1.

2.

3.

4.

PLATE a2

Holotype of *Betula fontinalis* Sarg.


HERBARIUM
OF THE
ARNOLD ARBORETUM
TENTH CENSUS OF THE UNITED STATES
DEPARTMENT OF FORESTRY
SILVA OF N. AMERICA.

PLATE a3

Type of <u>Betula</u> <u>obovata</u> Butler.

Type

FLORA OF MONTANA

B T BUTLER 190

(Sheet 1 of 2 Sheets)

PLATE a4

Type of *Betula hallii* Howell.

PLANTÆ OREGONENSES.

No.

Betula pumila. L

Oregon; coll ELIHU HALL, ann. 1871.

PLATE a5

Paratype of Betula resinifera Britton.

Betula
Janet Dugle

PLATE a6

Holotype of _Betula_ x _uliginosa_ (_B_. _resinifera_ x _B_. _pumila_ var. _glandulifera_) n. 'sp.' hyb.

Shrub 10-12' tall.

PLANTS OF ALBERTA
HERBARIUM—UNIVERSITY OF ALBERTA

1689A

Betula x uliginosa Dugle
(B. resinifera x B. pumila var. glandulifera)

Ponoka bog, 71 miles south of Edmonton.

August 13, 1961

TYPE

per J. R. Dugle

PLATE a7

Holotype of _Betula_ x _sargentii_ (_B_. _pumila_ var. _glandulifera_ x _B_. _glandulosa_) n. 'sp.' hyb.

Shrub 2-3' tall.


PLANTS OF ALBERTA
HERBARIUM—UNIVERSITY OF ALBERTA
TYPE
DET

PLATE a8

Isotype of _Betula_ x _eastwoodae_ Sarg. (_B_. _fontinalis_ x _B_. _glandulosa_)


UNITED STATES NATIONAL MUSEUM
Flora of the Yukon
Dawson, Canada
Betula Eastwoodae Sarg.
Isotype
Collected for THE ARNOLD ARBORETUM,
by Alice Eastwood
1914

PLATE a9

Holotype of *Betula* x *utahensis* Britton (*B*. *fontinalis* x *B*. *papyrifera*)


NEW YORK
BOTANICAL
GARDEN
Type

PLATE a10

Collection from the type tree of _Betula_ x _andrewsii_ A. Nels.

PLANTS OF COLORADO, U.S.A.

BETULA ? ANDREWSII A. Nels.
(This is the individual tree figured in the original description)

BOULDER CO.: Long Canyon, SW side of Green Mountain, foothills W of Boulder

11 Sept. 19[illegible]3 W. [illegible] [illegible]r

Herbarium of the University of Colorado
Boulder

PLATE all

Isotype of _Betula conmixta_ Sargent.

UNITED STATES NATIONAL MUSEUM

367 Flora of the Yukon
Dawson, Canada

Betula commixta Sarg.
Isotype
24 mile [illegible]

Collected for THE ARNOLD ARBORETUM,
by Alice Eastwood

[illegible] 1914

PLATE a12

Type of Betula montanensis Butler.


Type
FLORA OF MONTANA
B. T BUTLER
190

PLATE a13

Type of *Betula subcordata* Rydberg.


HERBARIUM
ARNOLD ARBORETUM
From
THE UNITED STATES NATIONAL HERBARIUM
PLANTS OF NORTHERN IDAHO
Betula occidentalis
Assistants.
A. A. HELLER,
SILVA OF N. AMERICA.

PLATE a14

Type of *Betula* x *arbuscula* n. 'sp.' hyb. (*B*. x *sargentii* x *B*. *papyrifera*)

Shrub 15-20' tall.

PLANTS OF ALBERTA
HERBARIUM—UNIVERSITY OF ALBERTA

1734

Betula x arbuscula Dugle
(B. x sargentii x B. papyrifera)

Mountain Creek at Pocahontas, Jasper National Park.

September 5, 1961

TYPE

DET J. R. Dugle

PLATE a15

Type of _Betula_ x _winteri_ n. 'sp.' hyb. (_B_. _papyrifera_ x _B_. _resinifera_)

Tree 35-40' tall.

PLANTS OF ALBERTA
HERBARIUM—UNIVERSITY OF ALBERTA

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

TYPE

DET.

PLATE a16

Type of _Betula_ _sandbergii_ Britton.

NEW YORK BOTANICAL GARDEN

Ex-Herb. J. H. SANDBERG. Type

Sandbergi Britton

Betula ~~fontinalis~~

Local. Hennepin Co. Minn

Habit. Swamps

Date. .. July 1890 No.

JHS

NEW YORK BOTANICAL GARDEN
HERBARIUM OF DR. H. E. HASSE
PURCHASED, 1896

PLATE a17

Meiotic Irregularities in Betula Staminate Catkins

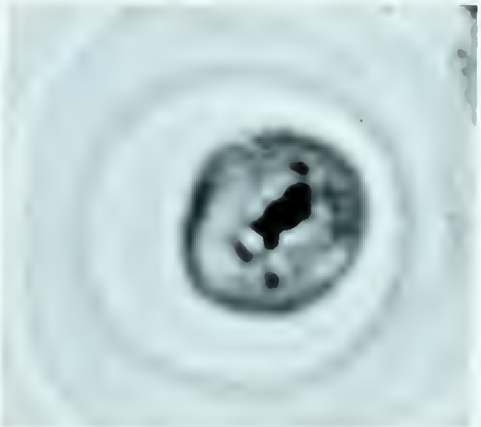


Fig. 1
Metaphase I, lagging chromosomes (B. papyrifera, 1695)

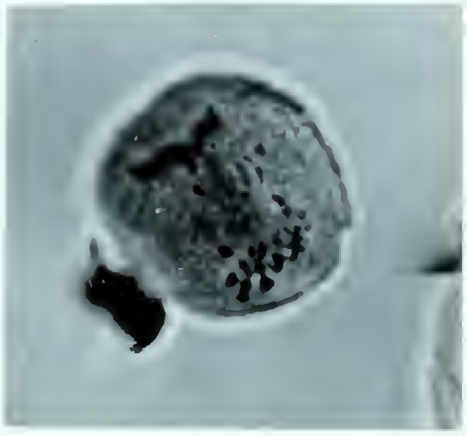


Fig. 2
Anaphase I, lagging chromosomes (B. papyrifera, 1695)

Fig. 3
Anaphase I, sticky chromosomes (B. resinifera, 2203)

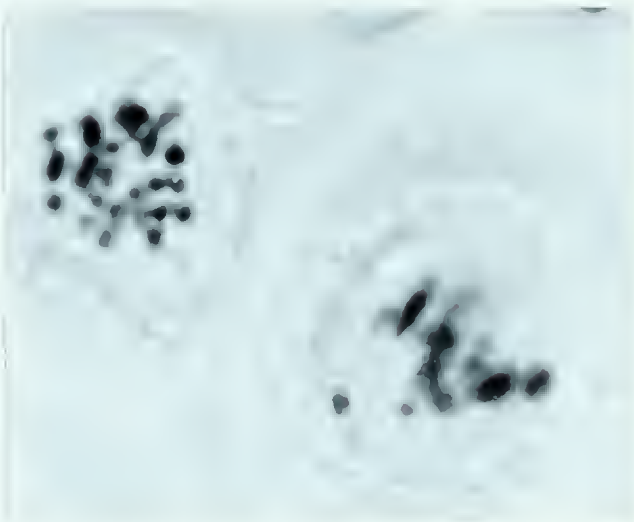


Fig. 4
Metaphase I, lagging chromosomes (B. pumila var. glandulifera, 2216)

FIGURE a18

Leaf Tracings of Ponoka Bog Birches

Leaves in the first row, upper left are *Betula pumila* var. *glandulifera* while those in the fifth row are *B. resinifera*. Those between are hybrids. All of the leaves are arranged in order of hybrid index from upper left to lower right.

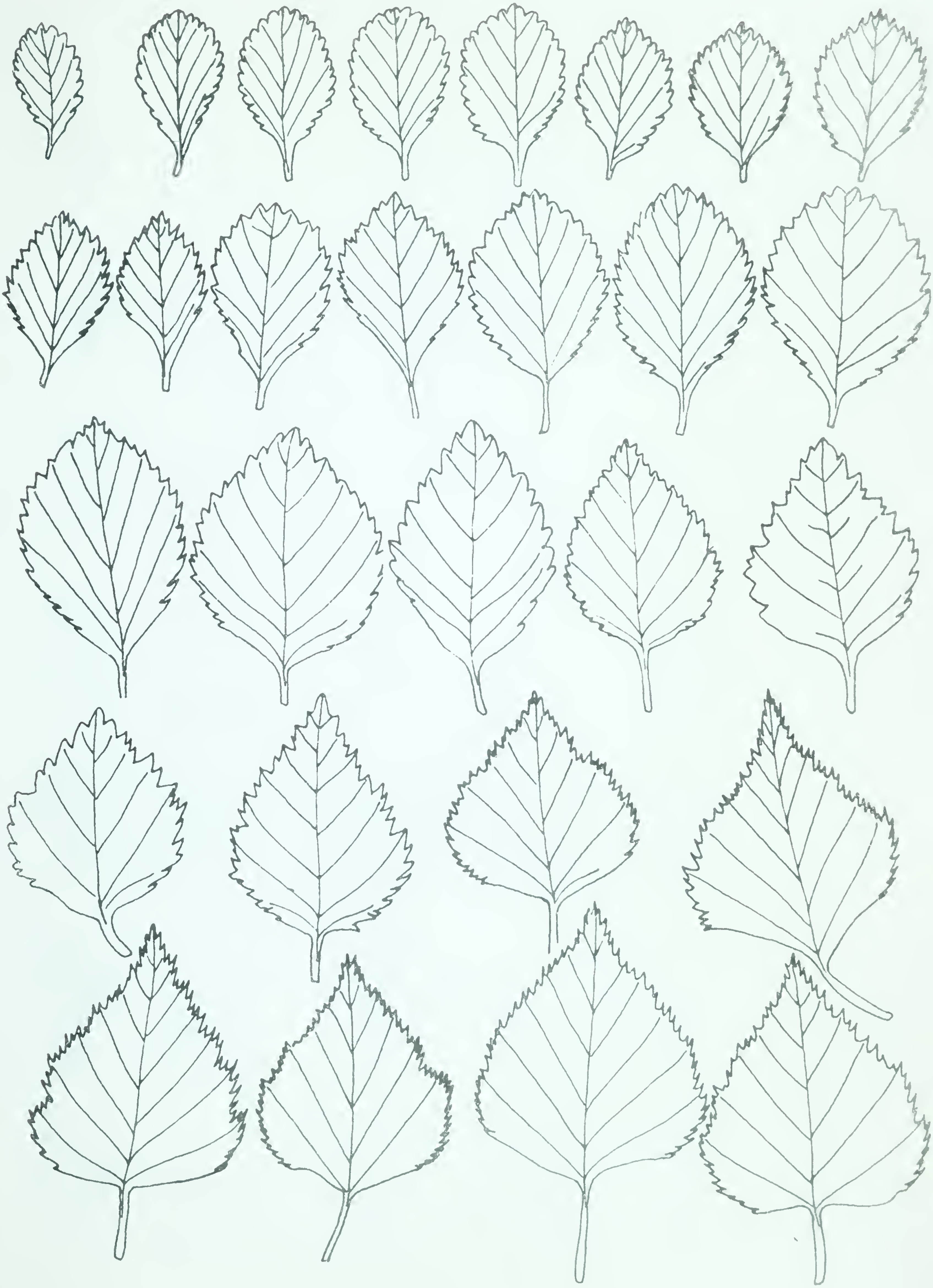


FIGURE a19

Bracts and Samaras of Ponoka Bog Birches (x 4)

The left column illustrates different individuals of *Betula pumila* var. *glandulifera*, the middle column *B*. x *uliginosa*, and the right column *B*. *resinifera*.

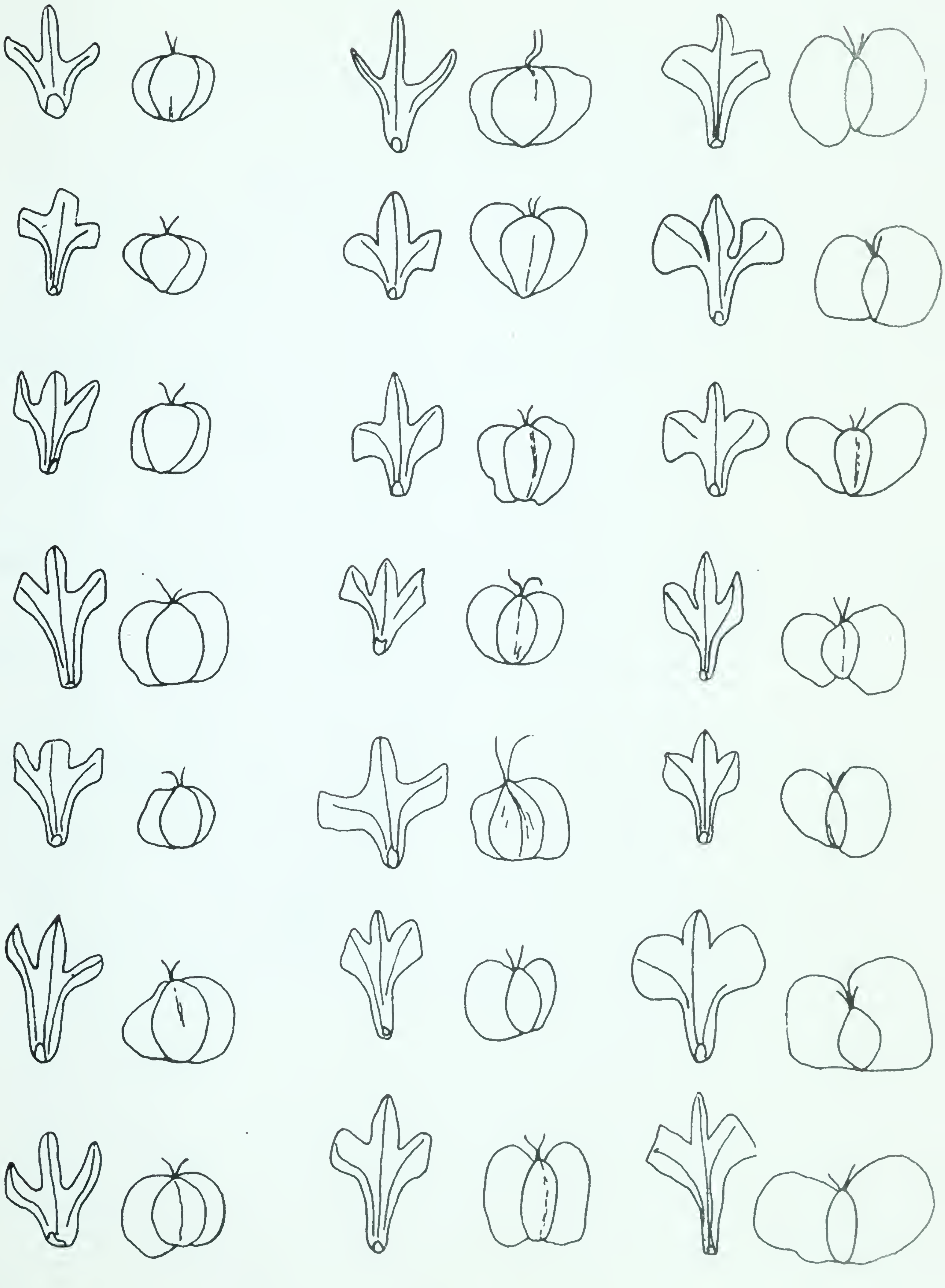


FIGURE a20

Key to the Polygonal Graphs of _Betula pumila_ var. _glandulifera_, _B. resinifera_, and hybrids: _LW_, leaf width in cm. _LL_, leaf length in cm. _WP_, widest point of leaf with relation to mid-line; 1 - widest point above mid-line, 2 - widest both above and at mid-line, 3 - widest at mid-line, 4 - widest below mid-line. _LT_, leaf tip; 1 - round, 2 - round-acute, 3 - acute, 4 - acuminate. _SW_, samara wing; 1 - much narrower than body, 2 - narrower than body, 3 - as broad as body, 4 - broader than body. _BC_, bark color and exfoliation; 1 - brown and non-exfoliating, 2 - brown and exfoliating, 3 - rose-gray and brown exfoliating, 4 - beige or pink-white exfoliating. _M_, margin of leaf; 1 - crenate, 2 - crenate-serrate, 3 - serrate, 4 - doubly-serrate. _NT_, number of teeth on one side of 5 leaves. _BL_, base of leaf; 1 - cuneate, 2 - round-cuneate, 3 - round-truncate, 4 - truncate. _NV_, number of pairs of lateral veins in leaf. _CW_, fruiting catkin width in mm. _CL_, fruiting catkin length in cm.

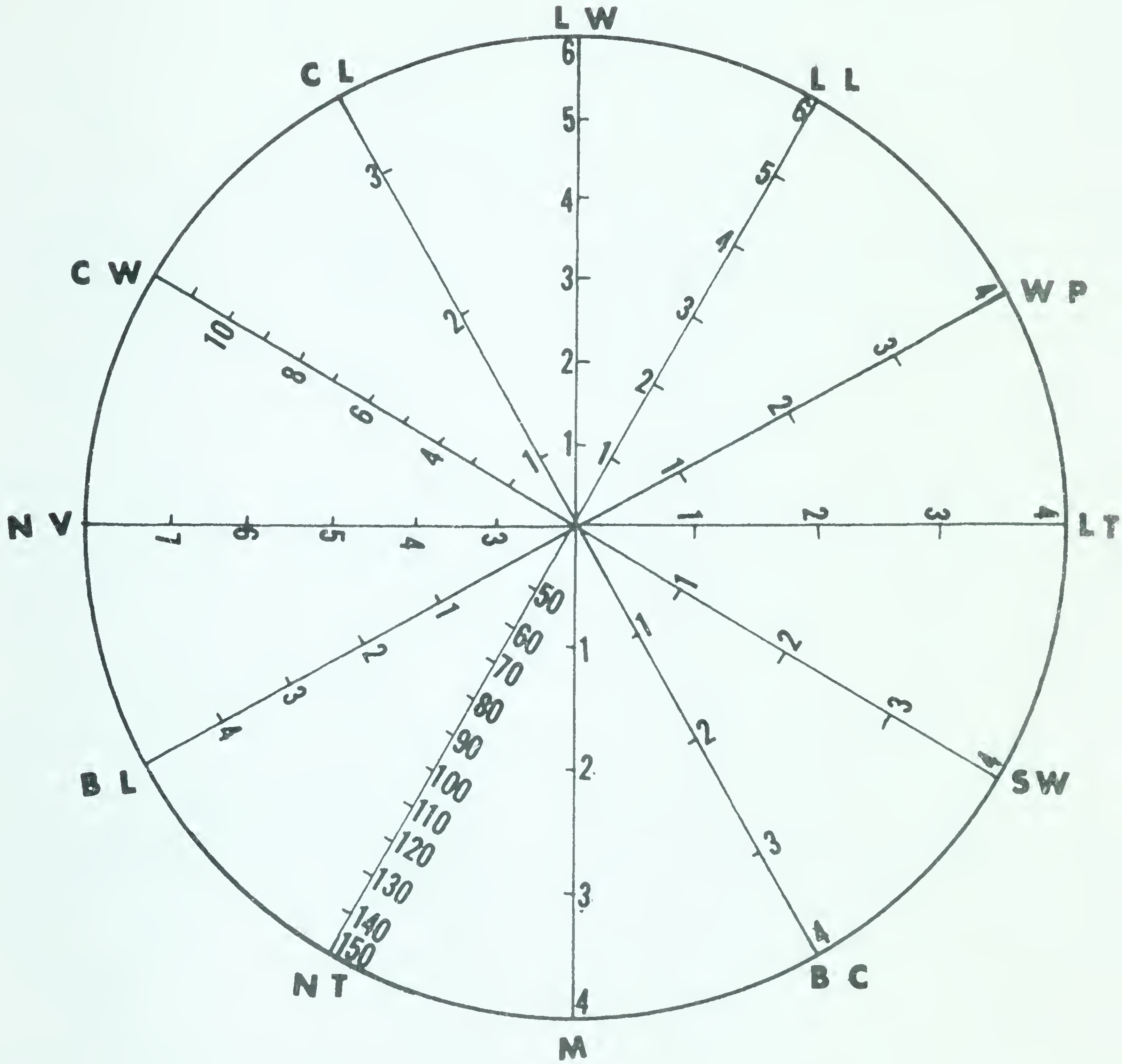
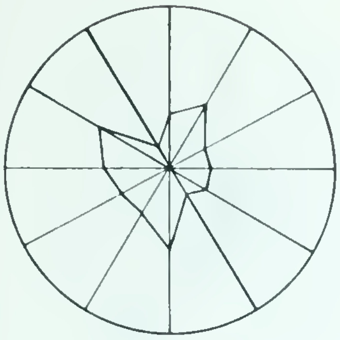

L W
C L
L L
C W
W P
N V
L T
B L
S W
N T
B C
M

FIGURE a21

Polygonal Graphs of Ponoka Bog Birches

These polygons are arranged to show successive increments in some characters from _Betula_ _pumila_ var. _glandulifera_ through the hybrids to _B_. _resinifera_. (See the following two pages.)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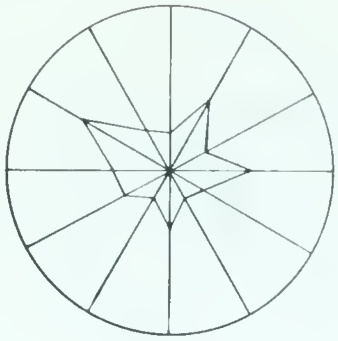
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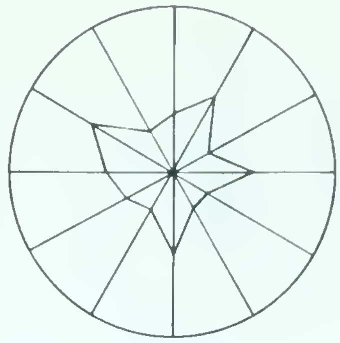
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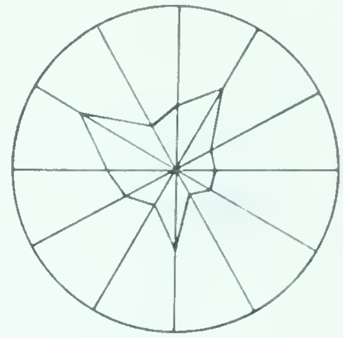
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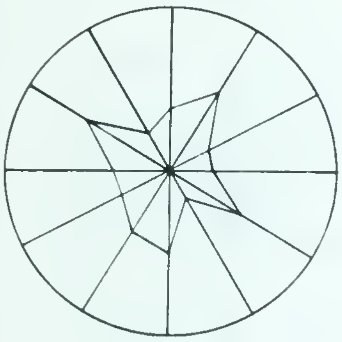
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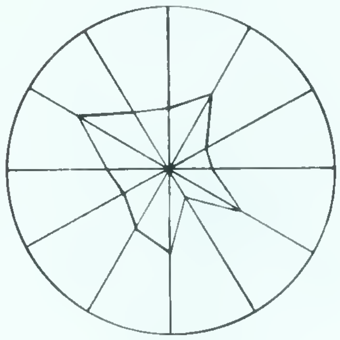
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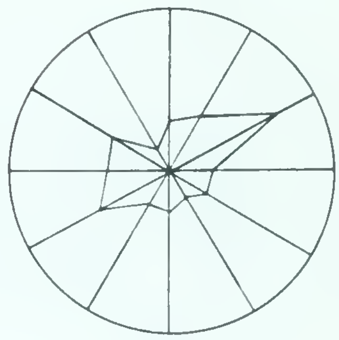
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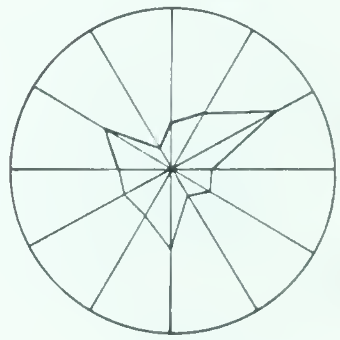
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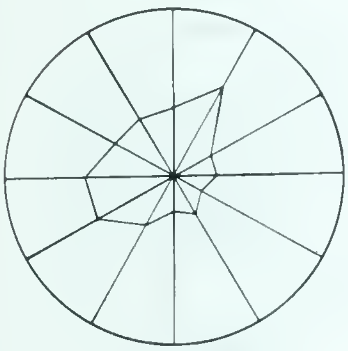
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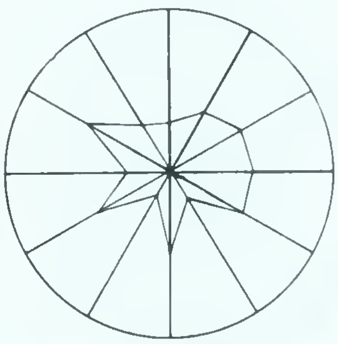
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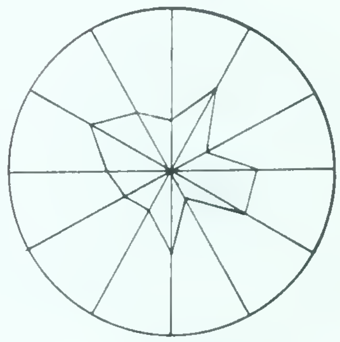
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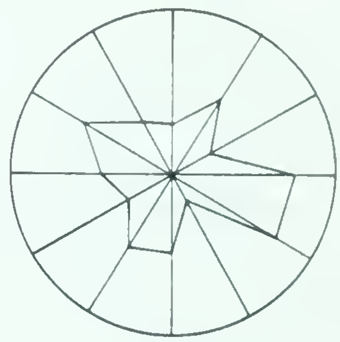
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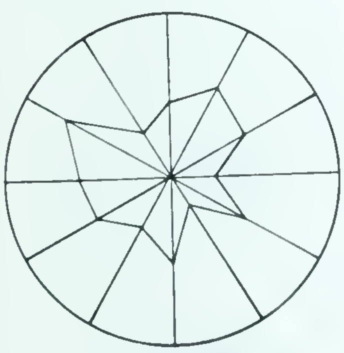
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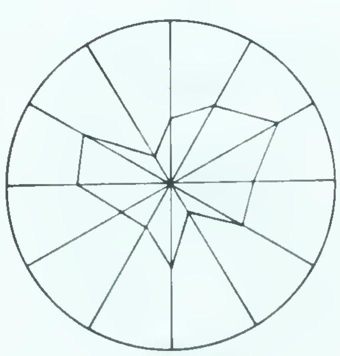
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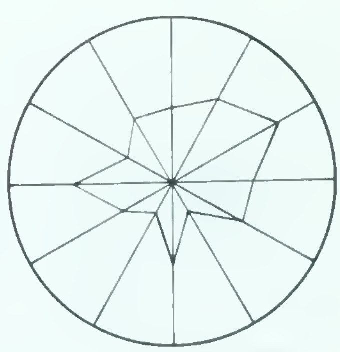
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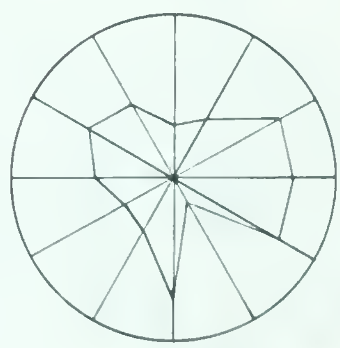
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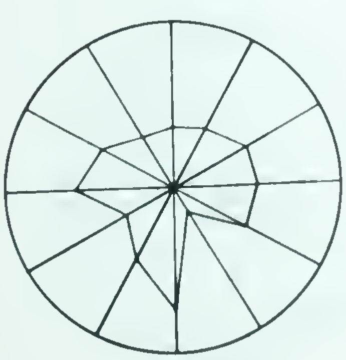
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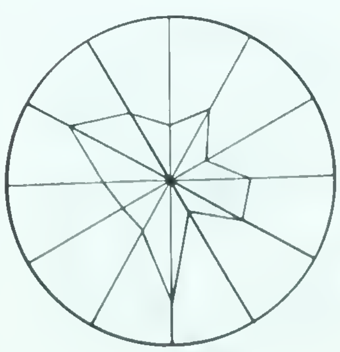
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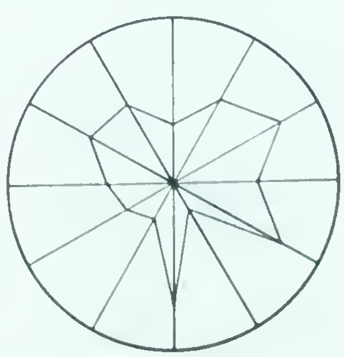
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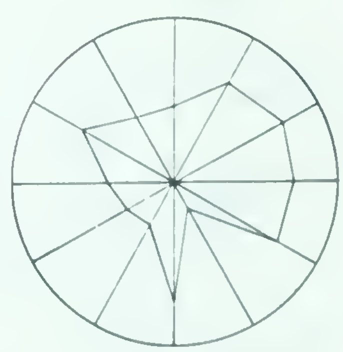
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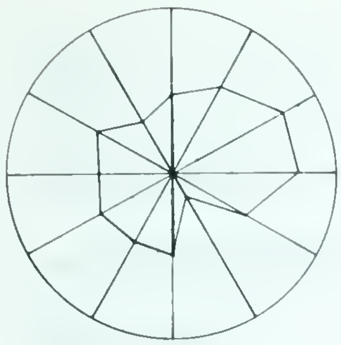
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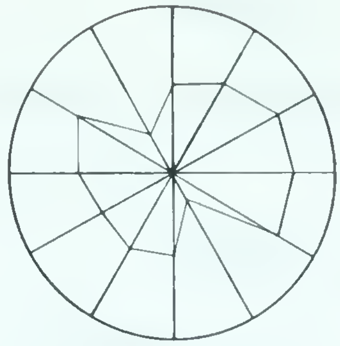
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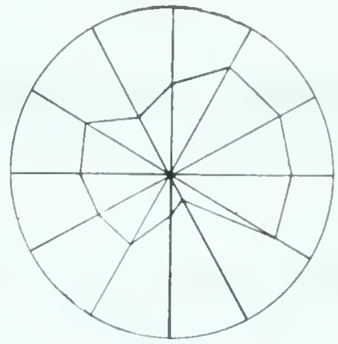
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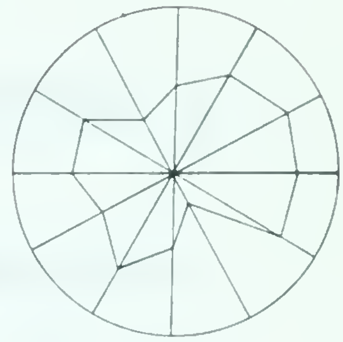
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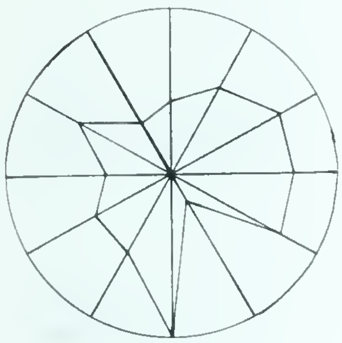
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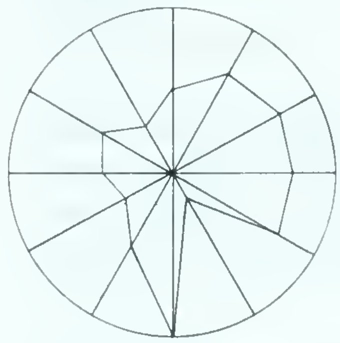
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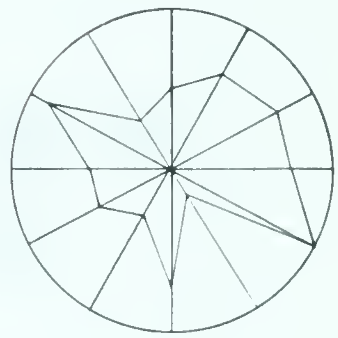
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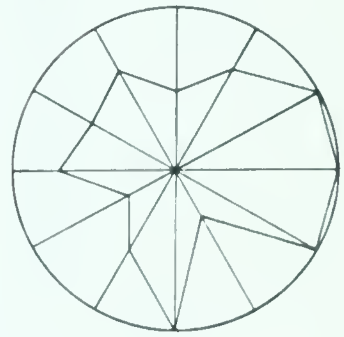
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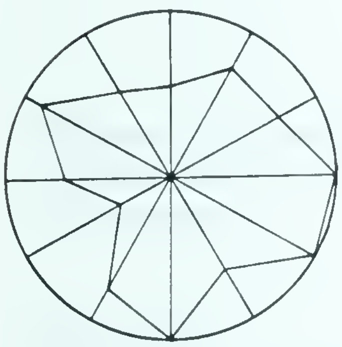
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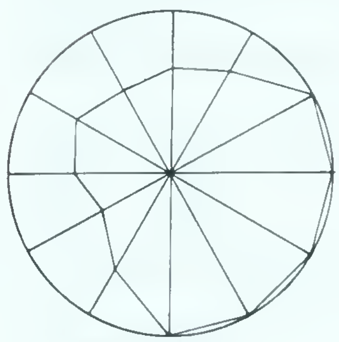
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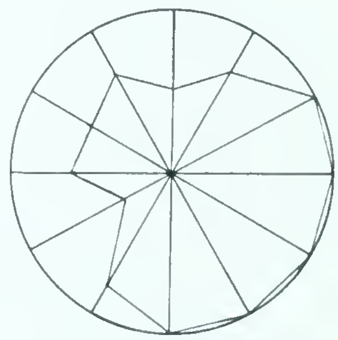
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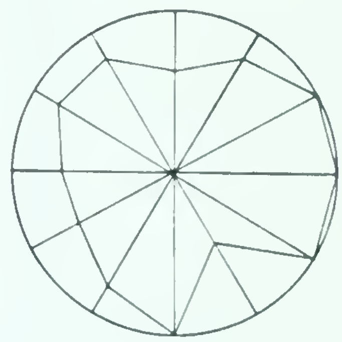
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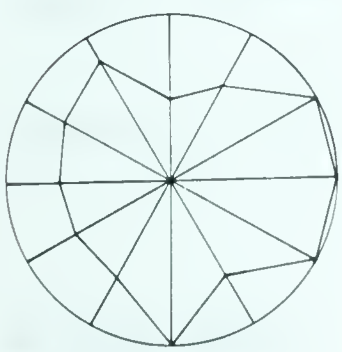
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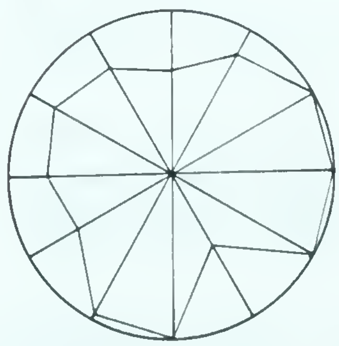
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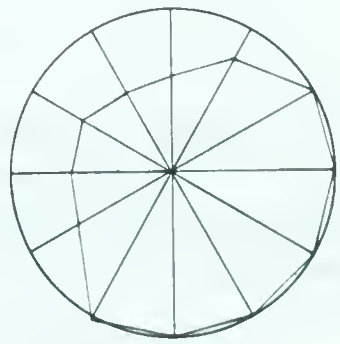
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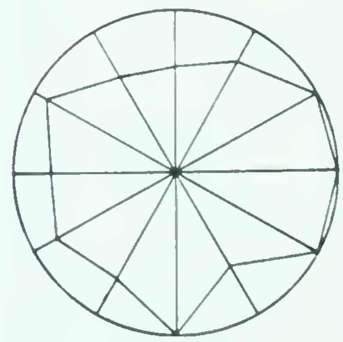
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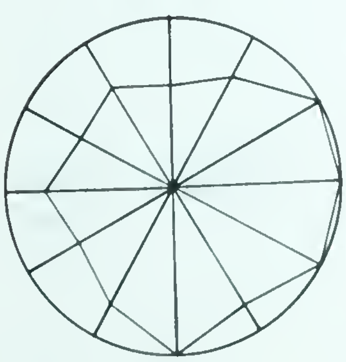
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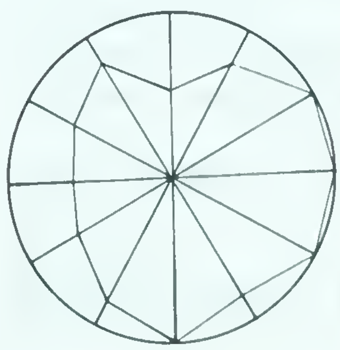
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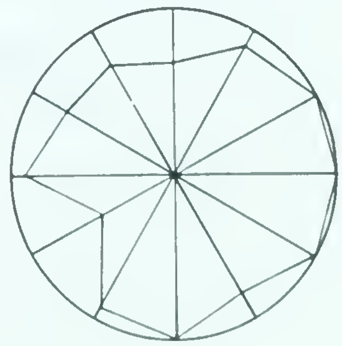
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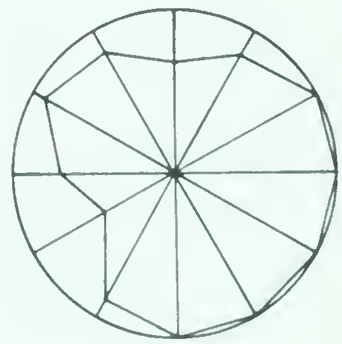
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TABLE a1

Hybrid index values of Betula pumila var. glandulifera, B. resinifera and hybrids.

Character	Range	Index number
Leaf tip	Round	0
	Round-acute	1
	Acute	2
	Acuminate	3
Fruit wing	Much narrower than body	0
	Narrower than body	1
	As broad as body	2
	Broader than body	3
Margin	Crenate	0
	Crenate-serrate	1
	Serrate	2
	Doubly-serrate	3
Number of teeth on one side of 5 leaves	Less than 70	0
	70 - 95	1
	96 - 120	2
	Greater than 120	3
Fruiting catkin length (cm)	Less than 2	0
	2 - 2.2	1
	2.3 - 2.5	2
	Greater than 2.5	3
Bark	Brown and non-exfoliating	0
	Brown and exfoliating	1
	Rose-gray and brown exfoliating	2
	Beige or pink-white exfoliating	3
Widest point on leaf	Widest above mid-line	0
	Widest both above and at mid-line	1
	Widest at mid-line	2
	Widest below mid-line	3
Leaf length (cm)	Less than 3	0
	3 - 4	1
	4.1 - 5	2
	Greater than 5	3

TABLE a2

Frequency distribution of mean stomatal length (μ) in Ponoka bog birches.

Size class (μ)	Number of individuals		
	Betula pumila var. glandulifera	Betula x uliginosa	Betula resinifera
16.1-17.0	-	-	1
17.1-18.0	-	1	-
18.1-19.0	-	-	4
19.1-20.0	-	1	2
20.1-21.0	-	3	2
21.1-22.0	1	1	5
22.1-23.0	-	-	1
23.1-24.0	-	1	1
24.1-25.0	1	3	2
25.1-26.0	-	3	-
26.1-27.0	1	4	-
27.1-28.0	2	-	-
28.1-29.0	1	2	-
29.1-30.0	2	3	-
30.1-31.0	2	-	-
31.1-32.0	3	-	-
32.1-33.0	1	-	-
Total	14	22	18

TABLE a3

Frequency distribution of mean pollen diameter (μ) in Ponoka bog birches.

Size class (μ)	Number of individuals		
	Betula pumila var. glandulifera	Betula x uliginosa	Betula resinifera
17.1-18.0	-	1	3
18.1-19.0	-	-	1
19.1-20.0	-	1	-
20.1-21.0	2	1	1
21.1-22.0	1	3	4
22.1-23.0	1	4	1
23.1-24.0	1	1	2
24.1-25.0	2	-	1
25.1-26.0	1	1	-
26.1-27.0	-	1	-
Total	8	13	13

FIGURE a22

Leaf Tracings of _Betula glandulosa_, _B_. _pumila_ var. _glandulifera_ and Hybrids

Leaves in the first row are _B_. _glandulosa_; those in the fourth row are _B_. _pumila_ var. _glandulifera_. Those between are hybrids.

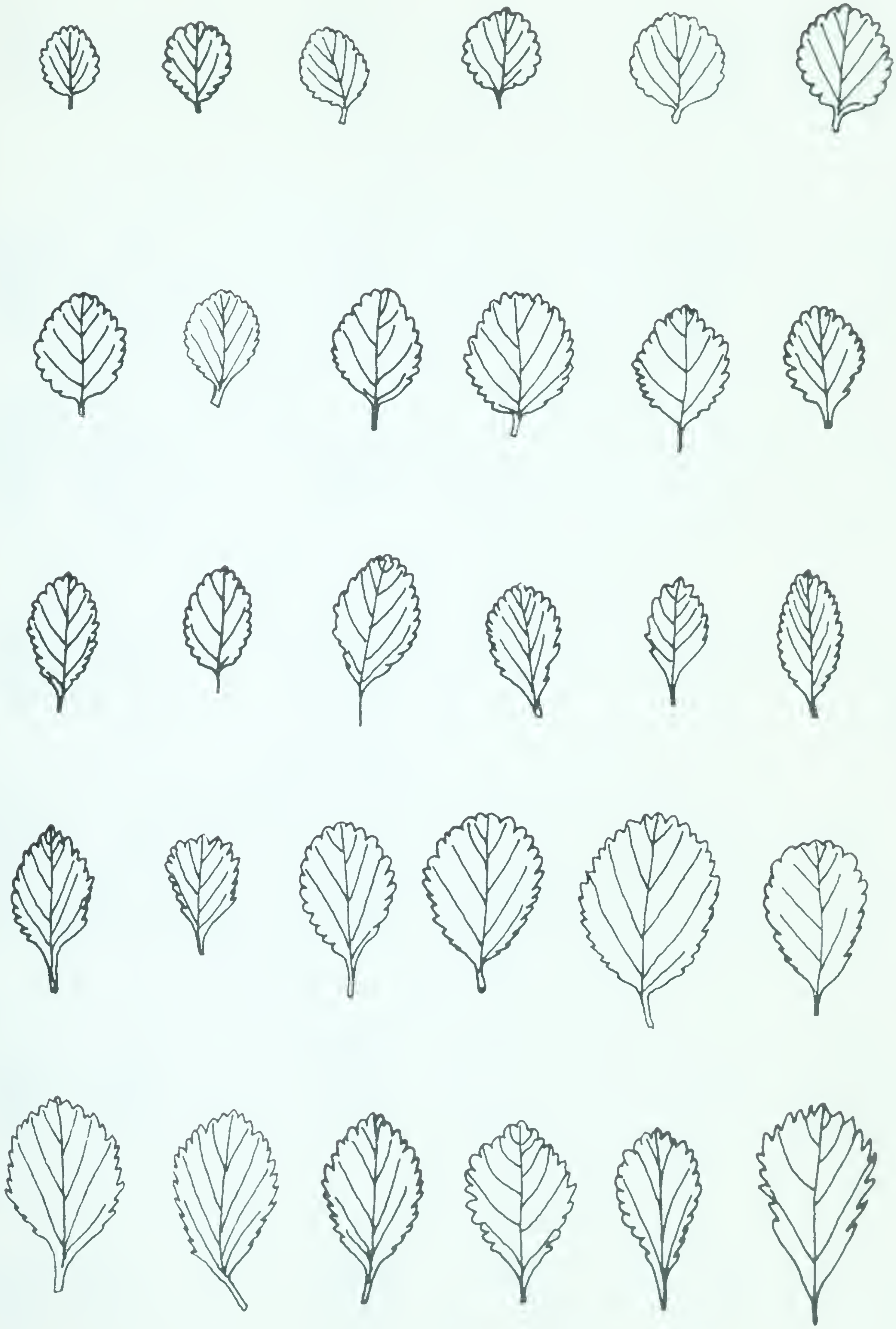


FIGURE a23

Bracts and Samaras of Betula glandulosa, B. pumila var. glandulifera, and Hybrids (x4)

These drawings are arranged vertically in order of hybrid index, beginning in top left.

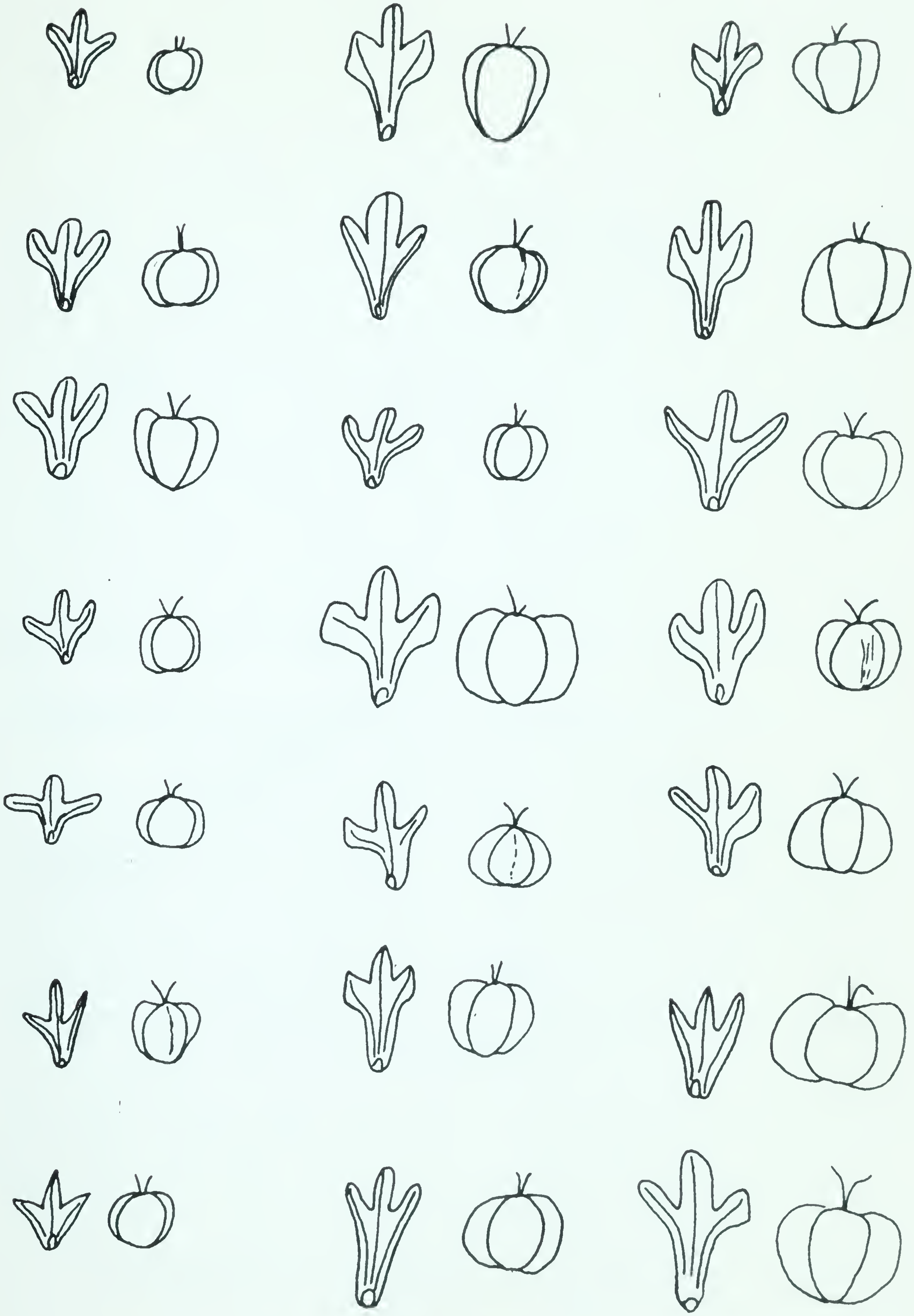
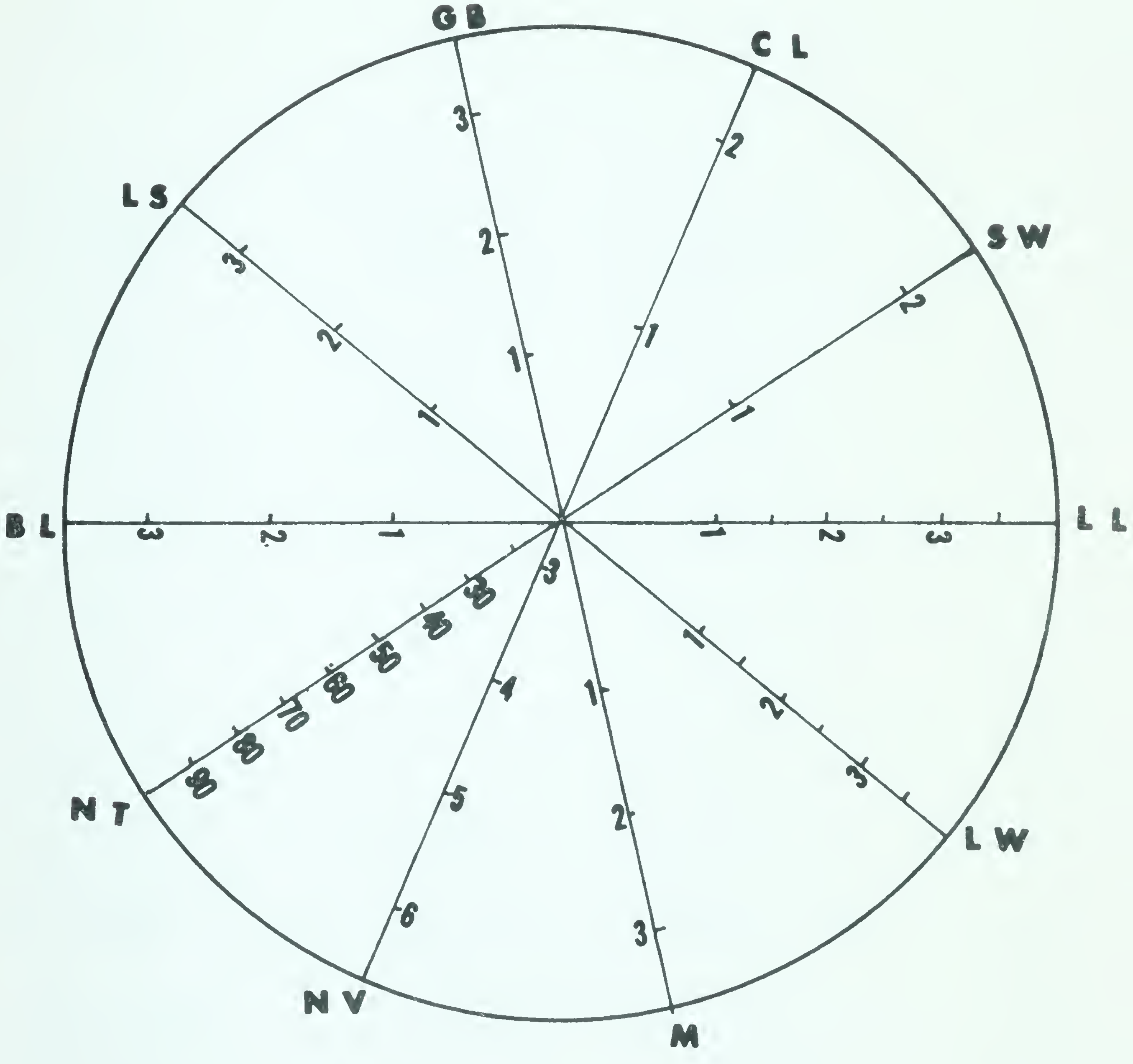


FIGURE a24

Key to the Polygonal Graphs of Betula glandulosa, B. pumila var. glandulifera, and Hybrids: GB, density of glands on branchlets; 1 - dense, 2 - scattered, 3 - sparse. CL, fruiting catkin length; 1 - less than 1 cm, 2 - more than 1 cm. SW, samara wing; 1 - less than ½ width of body, 2 - more than ½ width of body. LL, leaf length in cm. LW, leaf width in cm. M, margin of leaf; 1 - crenate, 2 - crenate-serrate, 3 - serrate. NV, number of pairs of lateral veins in leaf. NT, number of teeth on one side of 5 leaves. BL, base of leaf; 1 - round, 2 - round-cuneate, 3 - cuneate. LS, leaf shape; 1 - round, 2 - ovate, 3 - obovate.

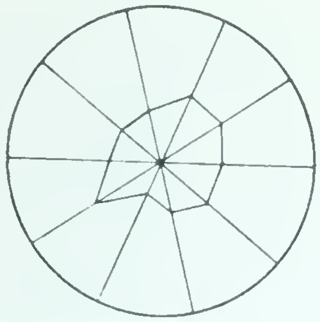


GB
CL
SW
LL
LW
M
NV
NT
BL
LS

FIGURE a25

Polygonal graphs of _Betula glandulosa_, _B. pumila_ var. _glandulifera_ and hybrids.

These polygons are arranged to show successive increments in some characters from _B. glandulosa_ through _B. x sargentii_ to _B. pumila_ var. _glandulifera_. (See the following two pages).



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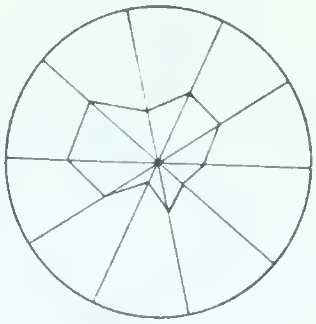

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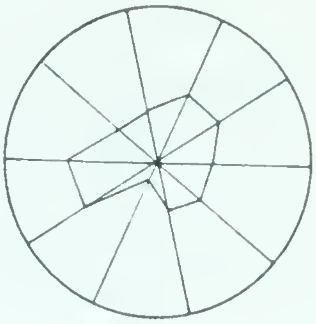

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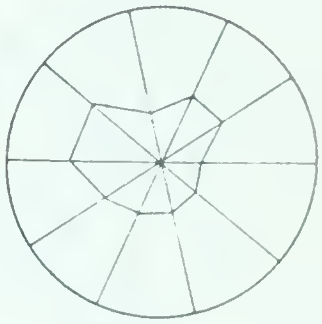

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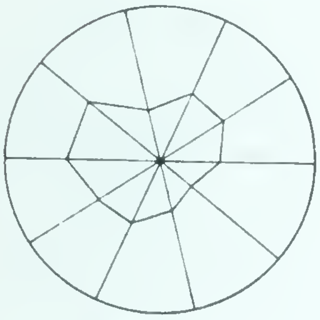

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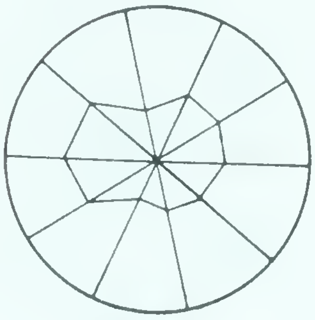

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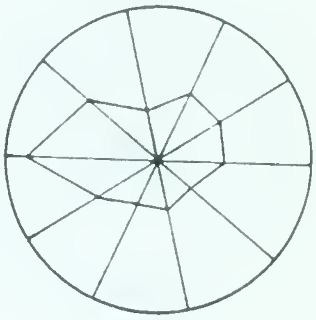

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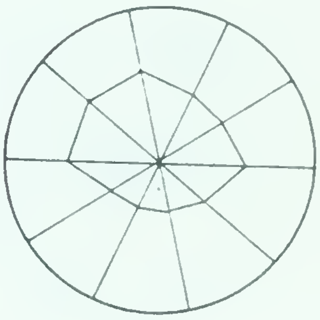

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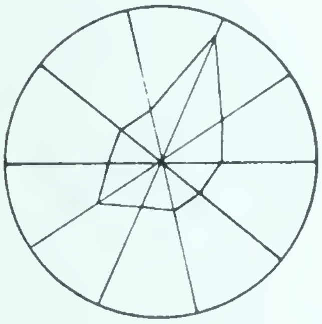

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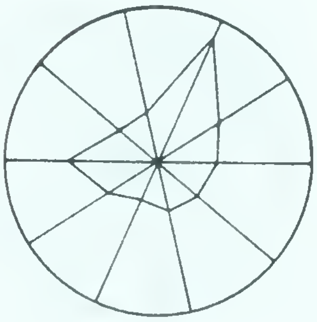

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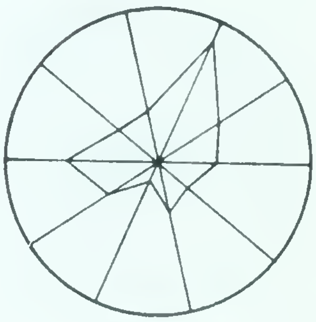

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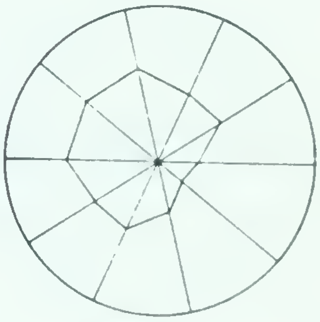

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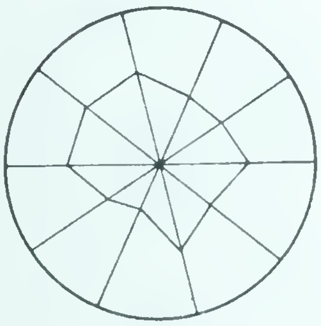

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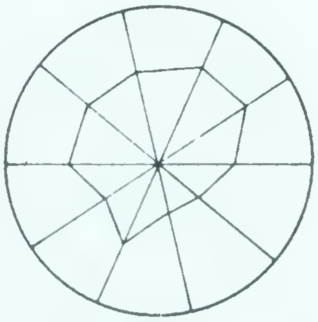

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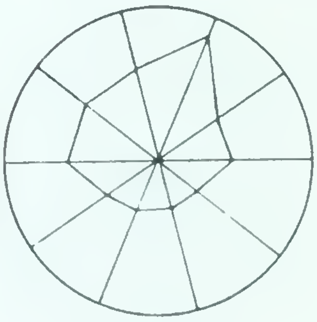

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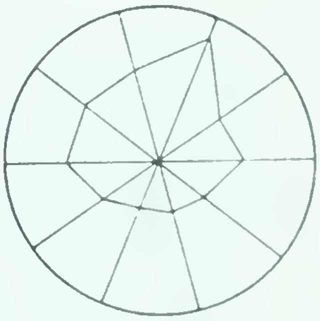

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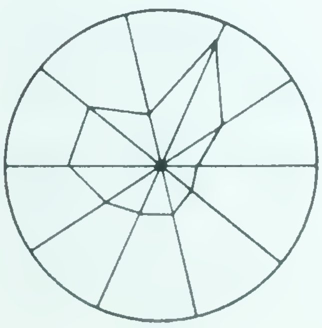

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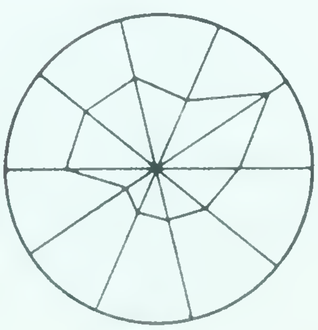

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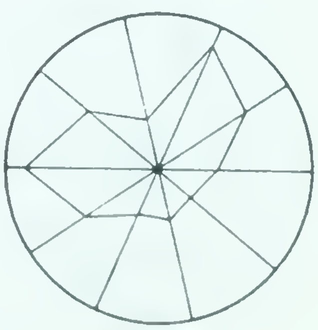

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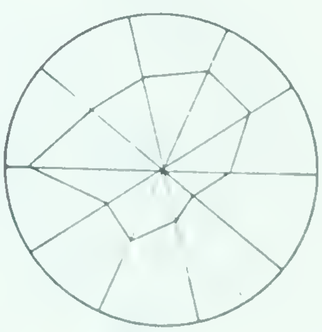

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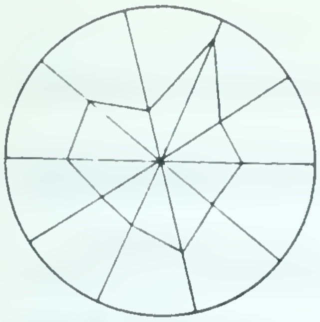
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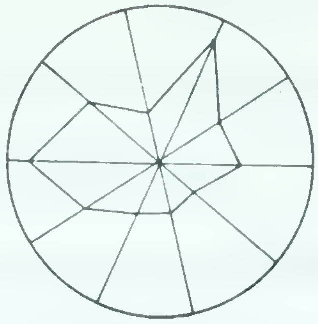
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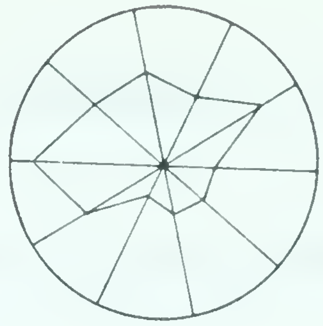
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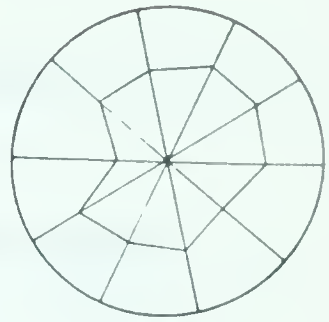
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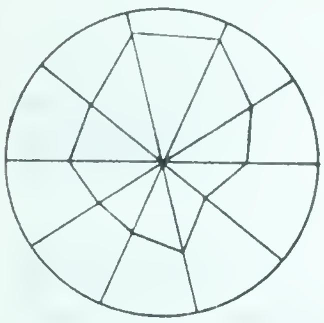
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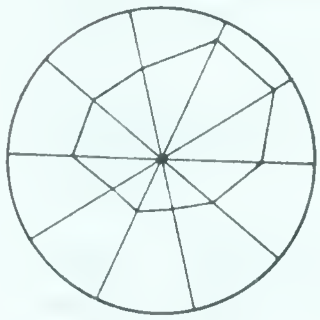
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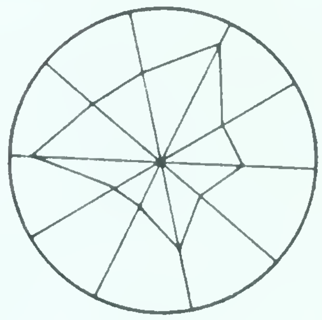
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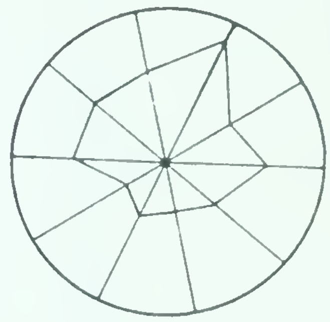
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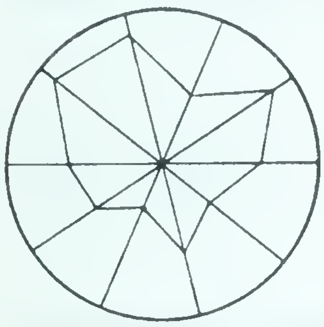
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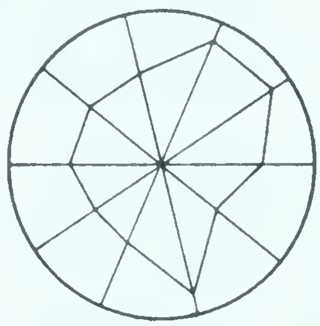
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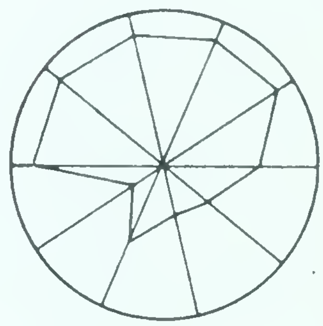
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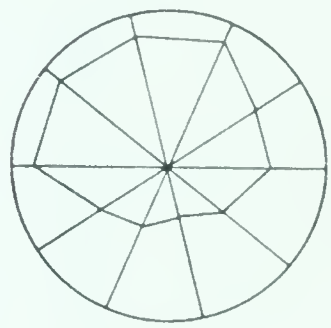
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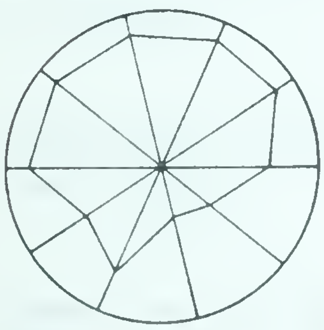
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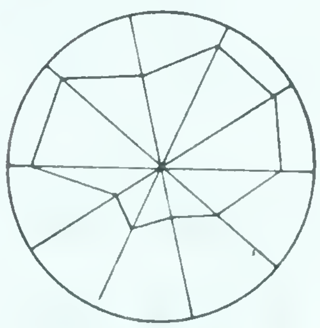
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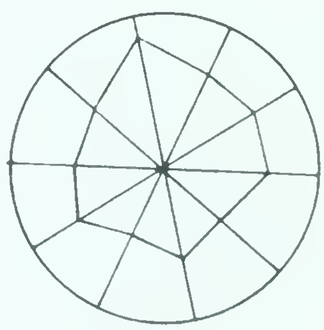
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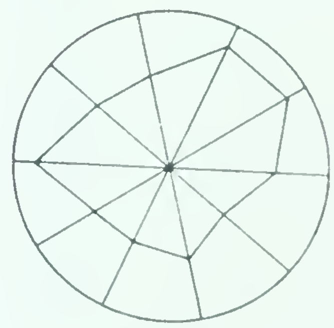
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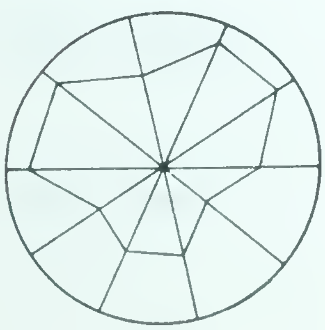
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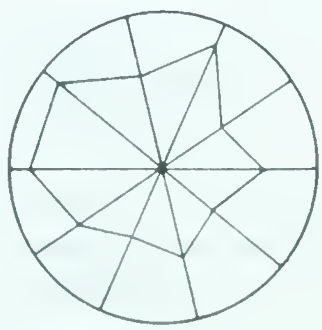
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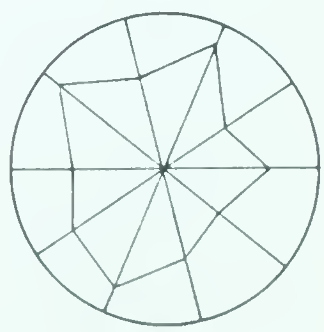
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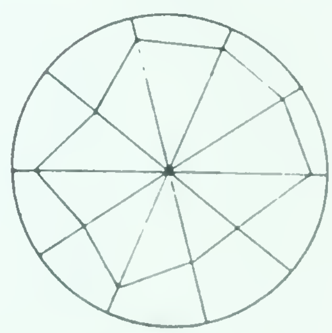
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TABLE a4

Hybrid index values of *Betula glandulosa*, *B. pumila* var. *glandulifera* and hybrids.

Character	Range	Index number
Leaf margin	Crenate	0
	Crenate-serrate	1
	Serrate	2
Branchlet glands	Dense	0
	Scattered	1
	Sparse	2
Fruiting catkin length	Less than 1 cm	0
	More than 1 cm	2
Leaf length (cm)	Less than 2	0
	2 - 2.5	1
	More than 2.5	2
Leaf width (cm)	Less than 1.5	0
	1.5 - 1.8	1
	More than 1.8	2
Number of teeth on one side of 5 leaves	Less than 50	0
	50 - 60	1
	61 - 70	2
	More than 70	3
Pairs of lateral leaf veins	3 - 4	0
	4.1 - 5	1
	More than 5	2
Samara wing *vs.* body	Less than ½	0
	More than ½	2
Leaf shape	Round	0
	Elliptic	1
	Obovate	2
Leaf base	Round	0
	Round-cuneate	1
	Cuneate	2

TABLE a5

Frequency distribution of mean stomatal length (μ) in *Betula glandulosa*, *B. pumila* var. *glandulifera*, and hybrids.

Size class (μ)	Number of individuals		
	B. glandulosa	*B.* x *sargentii*	*B. pumila* var. *glandulifera*
14.1-15.0	1	-	-
15.1-16.0	-	1	-
16.1-17.0	2	3	-
17.1-18.0	3	3	-
18.1-19.0	1	2	1
19.1-20.0	4	7	-
20.1-21.0	3	12	-
21.1-22.0	7	16	-
22.1-23.0	1	7	1
23.2-24.0	1	13	5
24.1-25.0	1	11	1
25.1-26.0	-	5	2
26.1-27.0	-	7	1
27.1-28.0	-	-	-
28.1-29.0	-	2	2
29.1-30.0	-	-	1
Total	24	89	14

FIGURE a 26

Leaf tracings of *Betula fontinalis*, *B. glandulosa* and hybrids.

Leaves in the first row, upper left are *B. glandulosa*; those in the fourth row are *B. fontinalis*. Those between are hybrids.

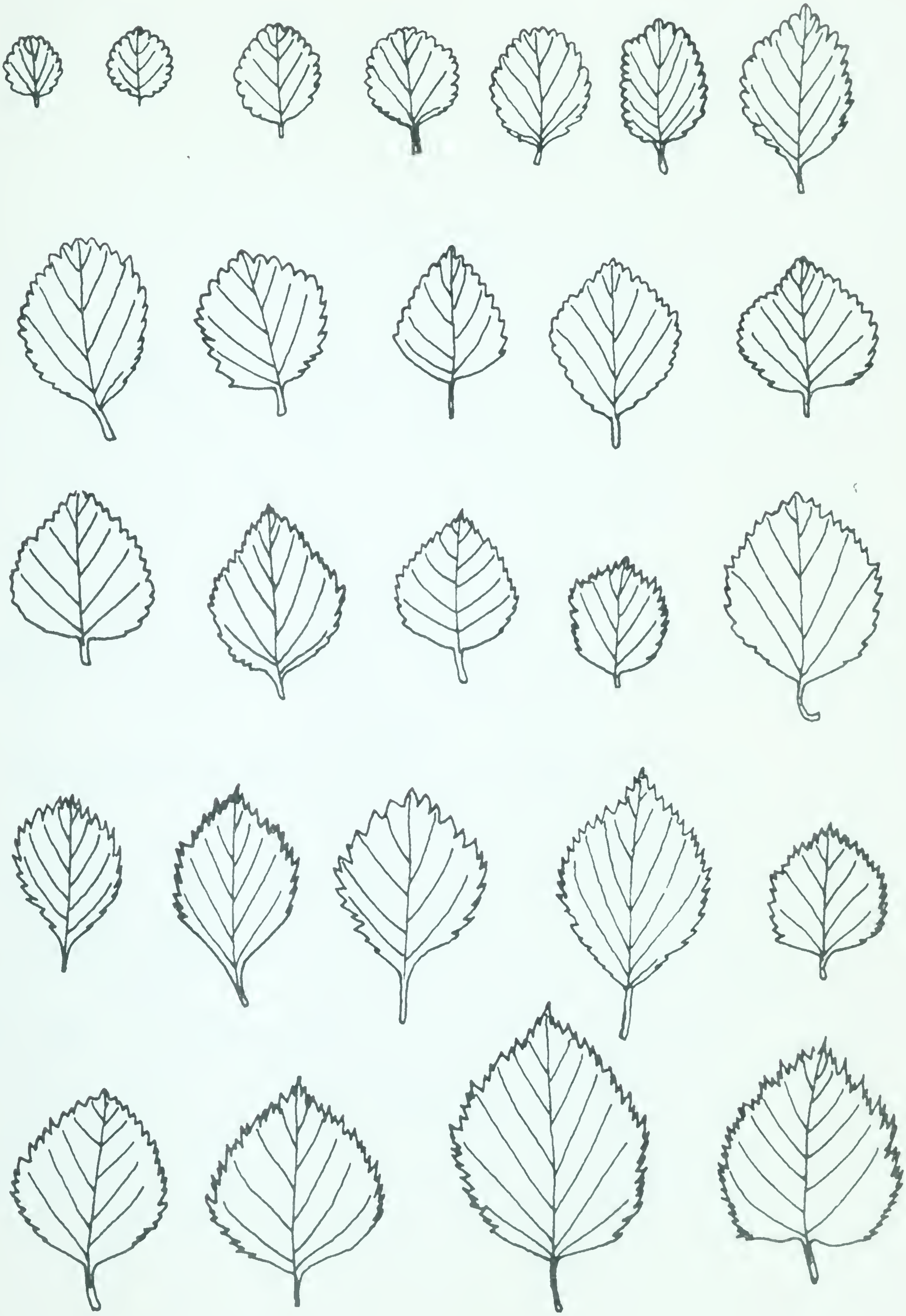
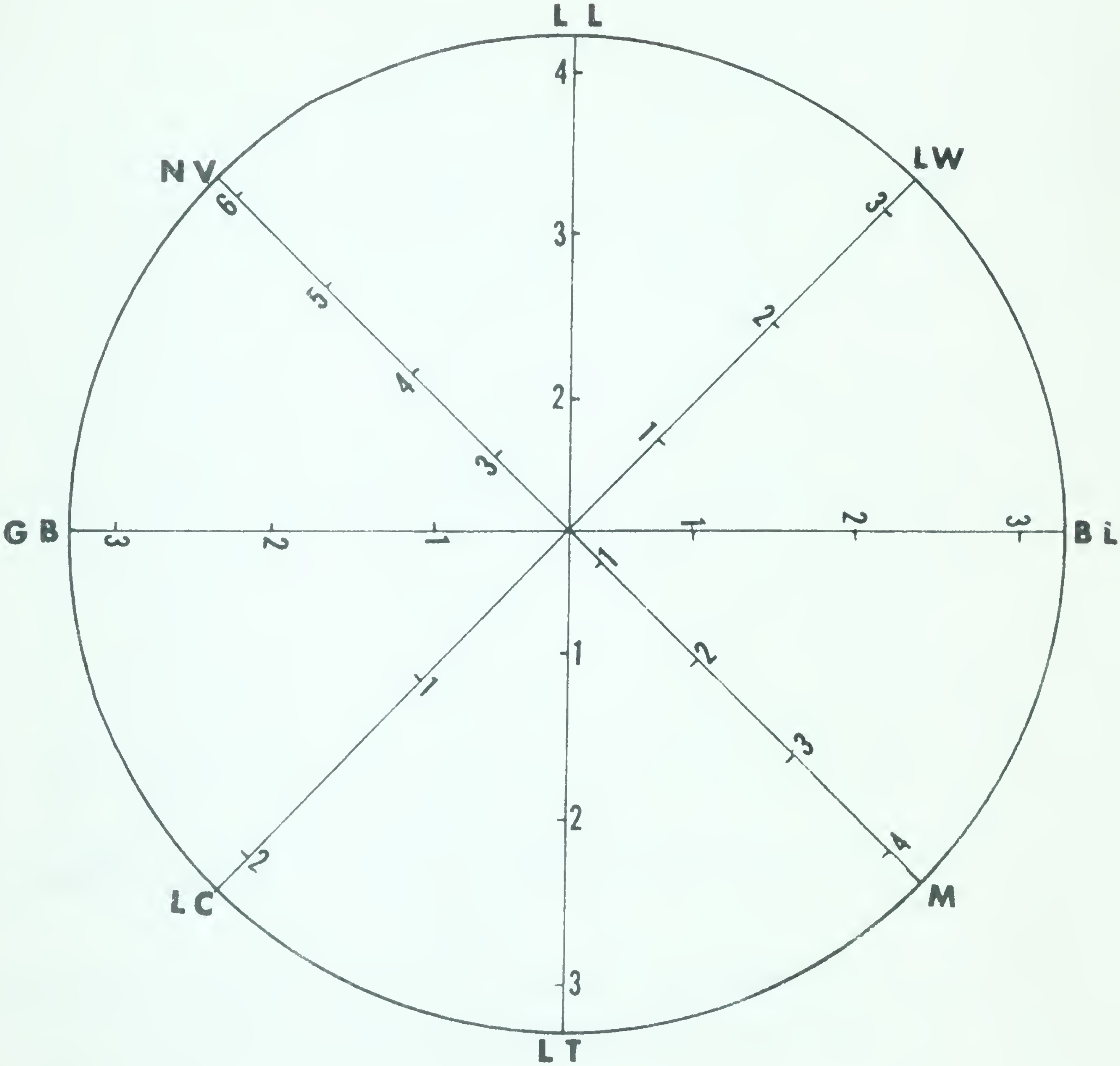


FIGURE a27

Key to the Polygonal Graphs of Betula glandulosa, B. fontinalis, and Hybrids:

LL, leaf length in cm. LW, leaf width in cm. BL, base of leaf; 1 - cuneate, 2 - cuneate-truncate, 3 - truncate. M, margin of leaf; 1 - crenate, 2 - crenate-serrate, 3 - serrate, 4 - doubly-serrate. LT, leaf tip; 1 - round, 2 - round-acute, 3 - acute. LC, leaf character; 1 - dull, 2 - shiny. GB, color of glands on branchlets; 1 - white, 2 - yellow, 3 - red. NV, number of pairs of lateral veins in leaf.

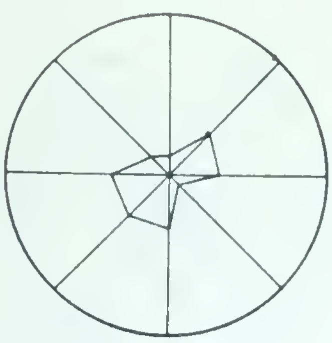


L L
LW
B L
M
L T
L C
G B
N V

FIGURE a28

Polygonal graphs of *Betula fontinalis*, *B. glandulosa* and hybrids.

The polygons are arranged to show successive increments in some characters from *B. glandulosa* through *B. x eastwoodae* to *B. fontinalis*. (See the following three pages).



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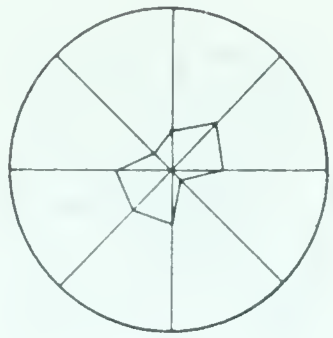

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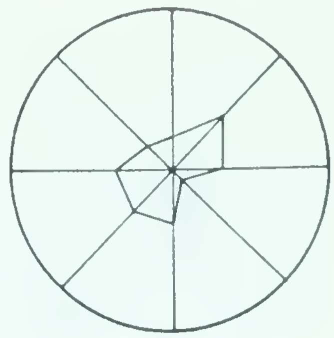

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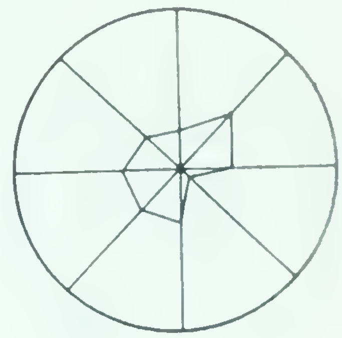

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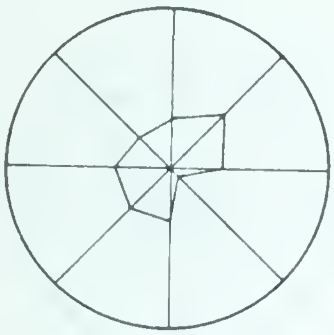

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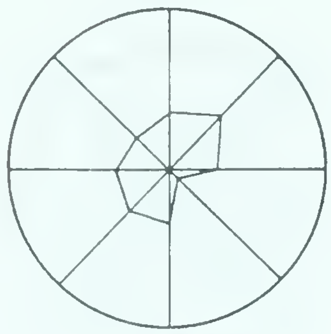

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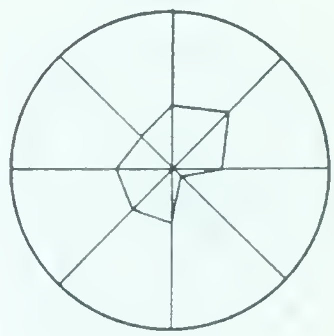

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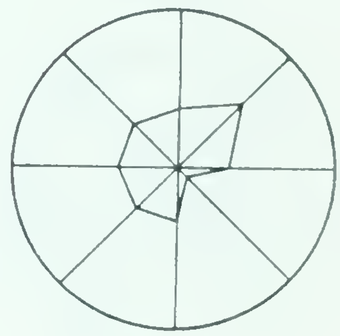

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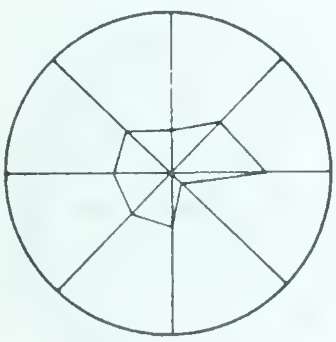

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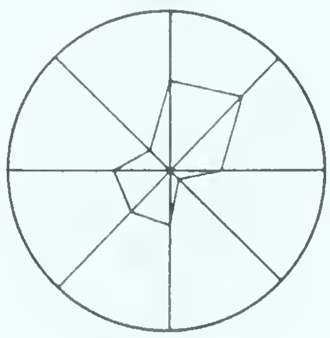

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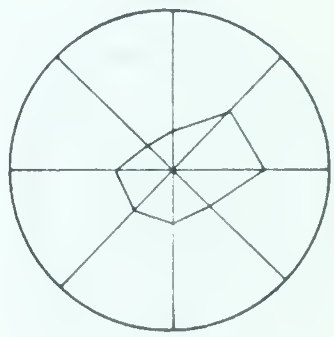

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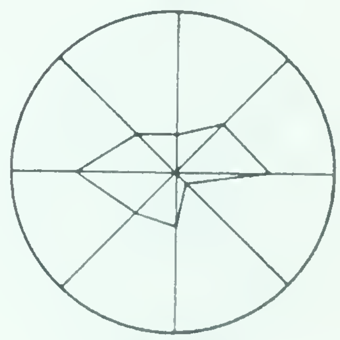

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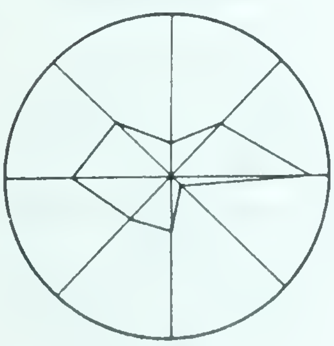

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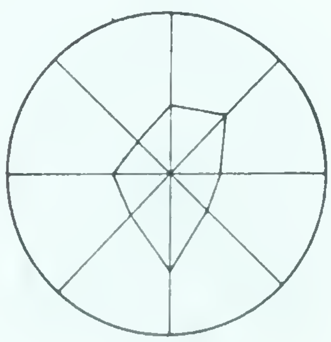

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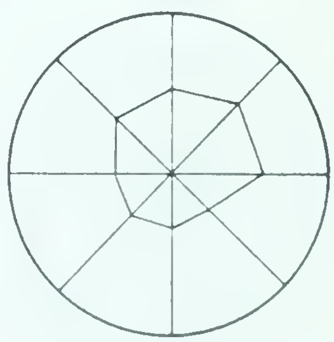

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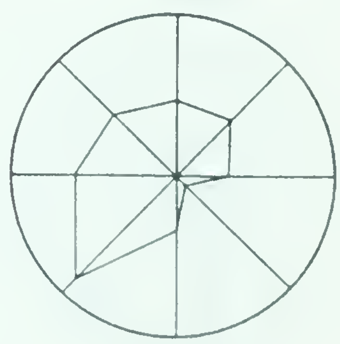

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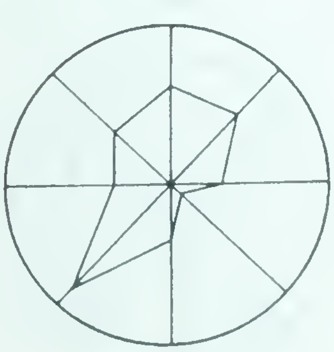

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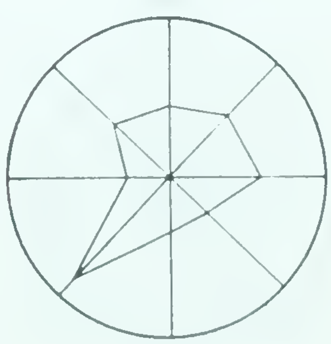

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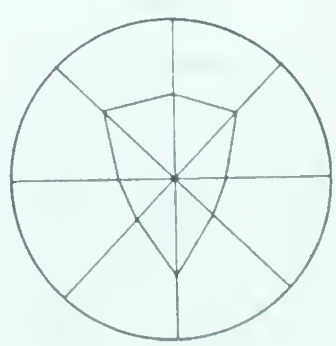

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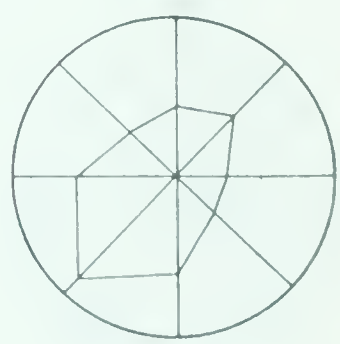

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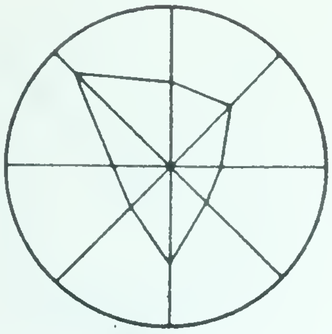

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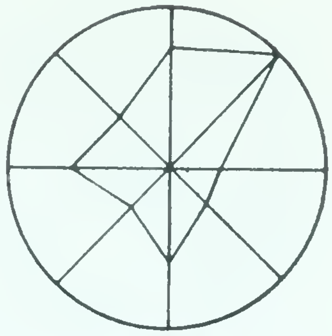

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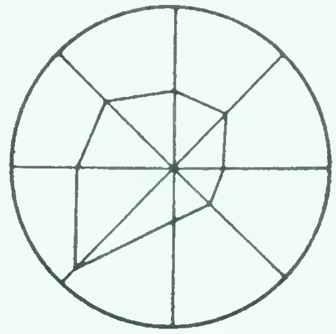

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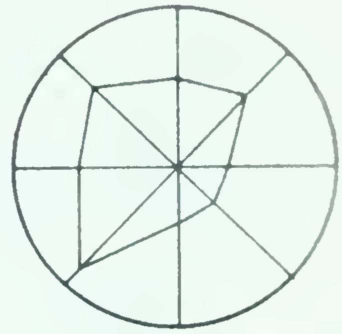

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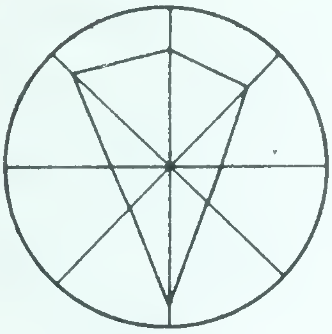

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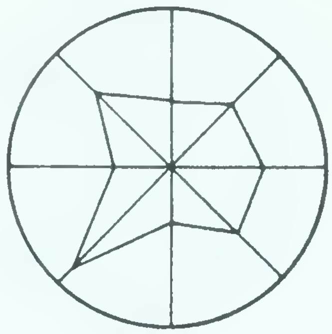

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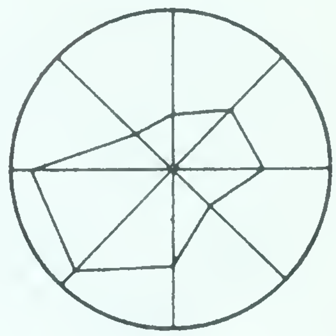

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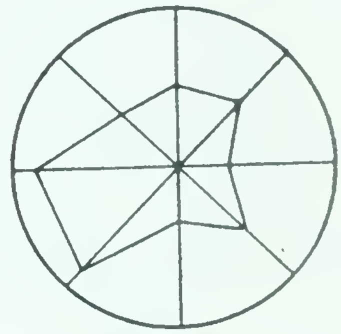

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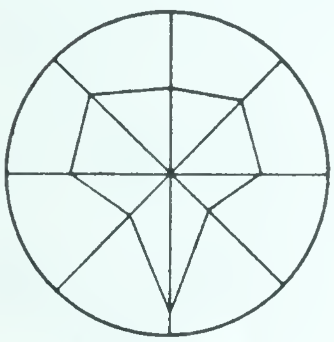

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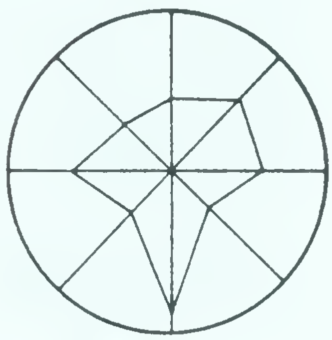

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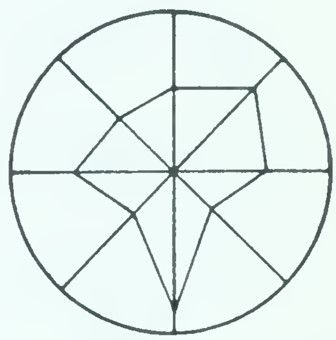

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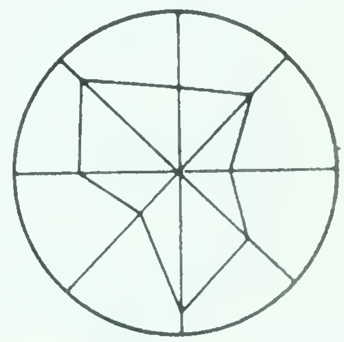

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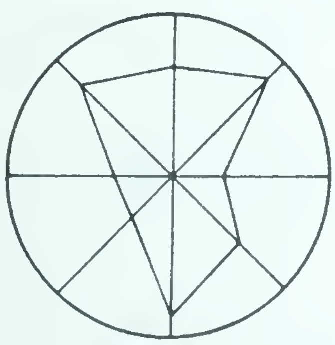

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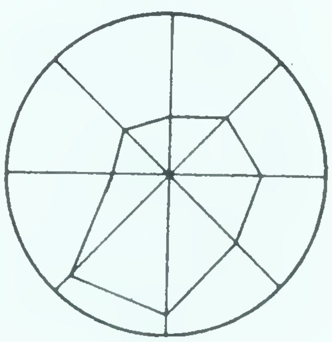

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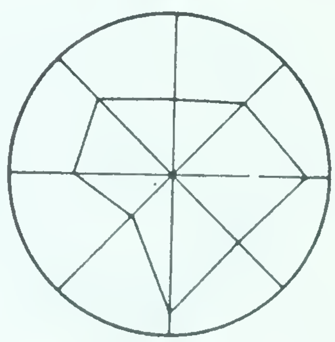

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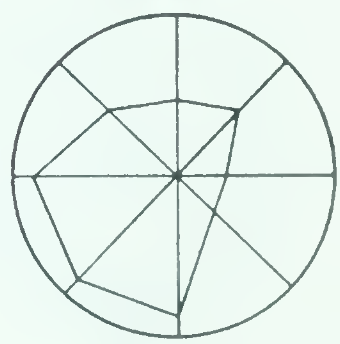

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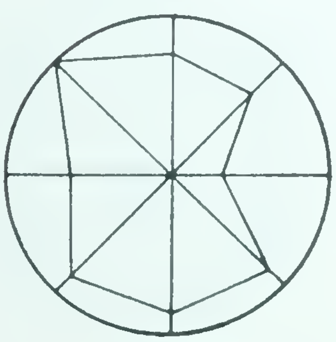

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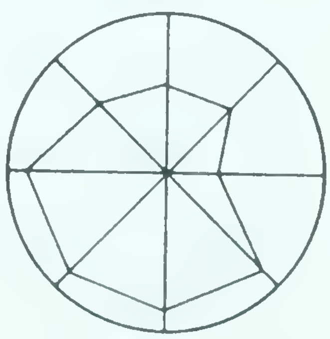

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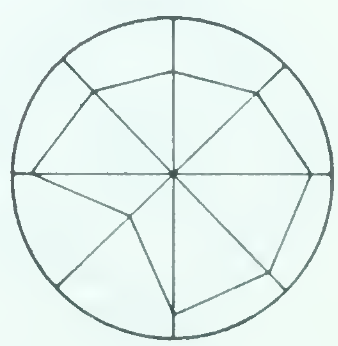

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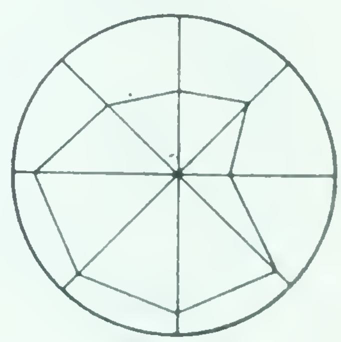

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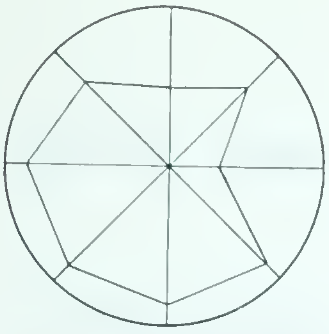

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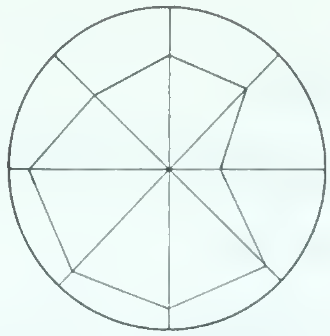

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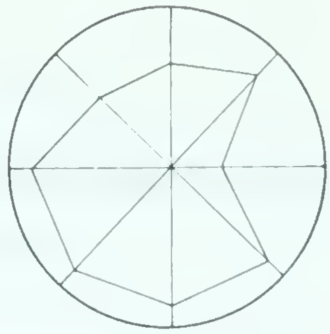

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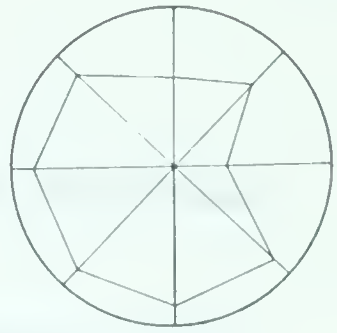

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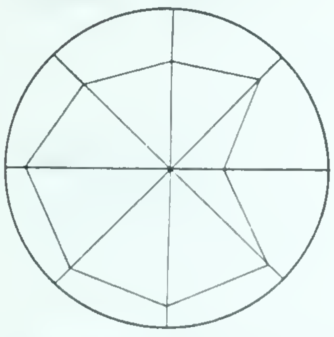

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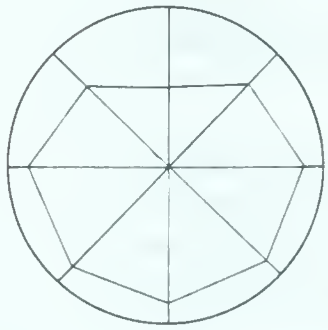

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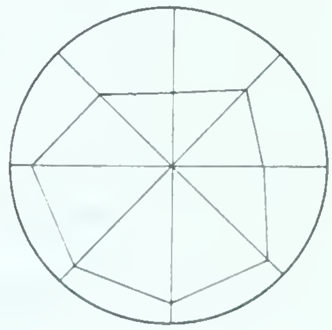

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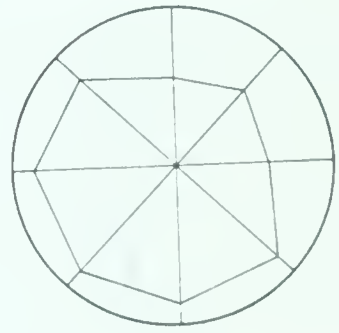

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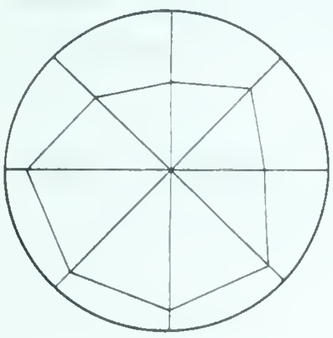

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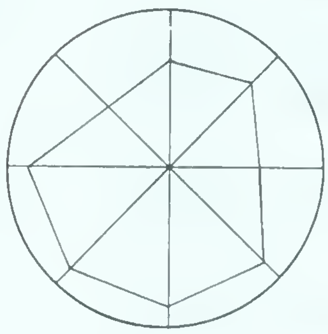

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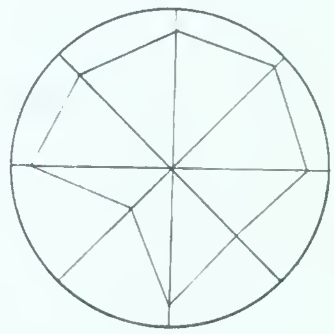

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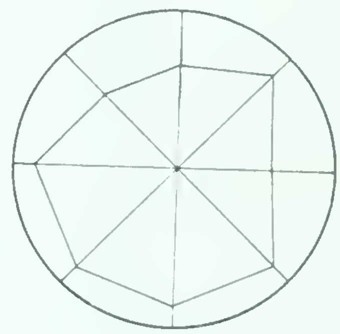

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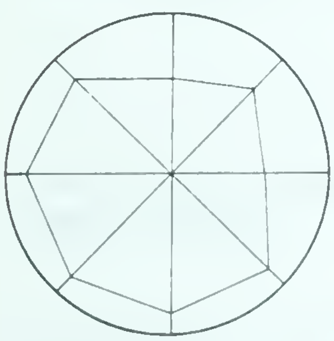

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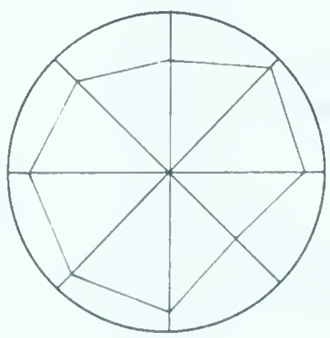

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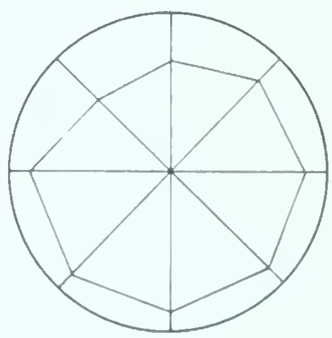

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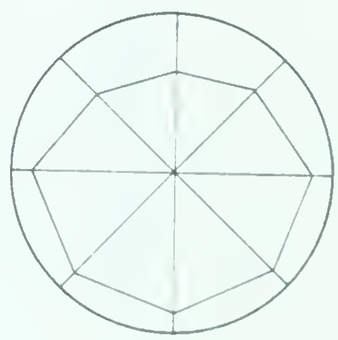

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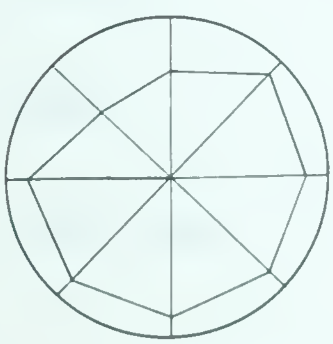

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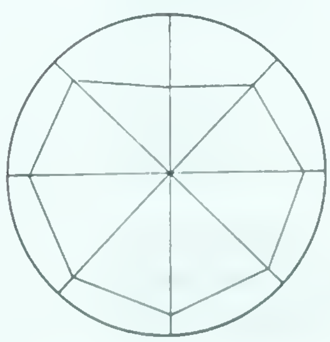

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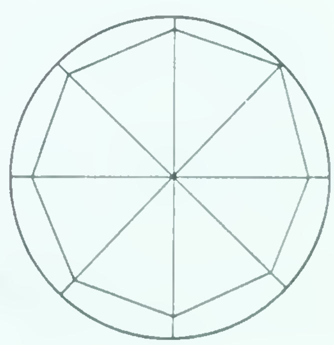

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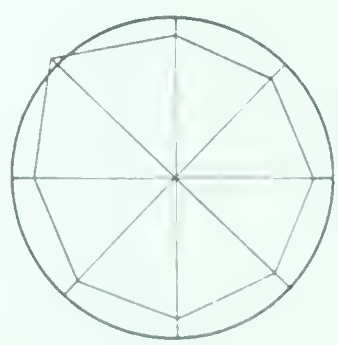


1939

TABLE a6

Hybrid index values of <u>Betula glandulosa</u>, <u>Betula fontinalis</u> and hybrids.

Character	Range	Index number
Leaf tip	Round	0
	Round-acute	1
	Acute	2
Margin	Crenate	0
	Crenate-serrate	1
	Serrate	2
	Doubly-serrate	3
Number of teeth on one side of five leaves	Less than 75	0
	75 - 99	1
	100 - 123	2
	More than 123	3
Leaf length (cm)	Less than 2	0
	2 - 3	1
	3.1 - 4	2
	More than 4	3
Leaf width (cm)	Less than 1.5	0
	1.5 - 2	1
	2.1 - 2.5	2
	More than 2.5	3
Pairs of lateral leaf veins	3 - 4	0
	4.1 - 5	1
	More than 5	2
Branchlet gland color	White	0
	Yellow	1
	Red	2
Leaf	Dull	0
	Shiny	2
Leaf base	Cuneate	0
	Round-cuneate	1
	Truncate	2

FIGURE a29

Leaf tracings of Betula fontinalis, B. papyrifera and hybrids.

Leaves in the first row, upper left are B. fontinalis while those in the third row are B. papyrifera. Those between are hybrids.

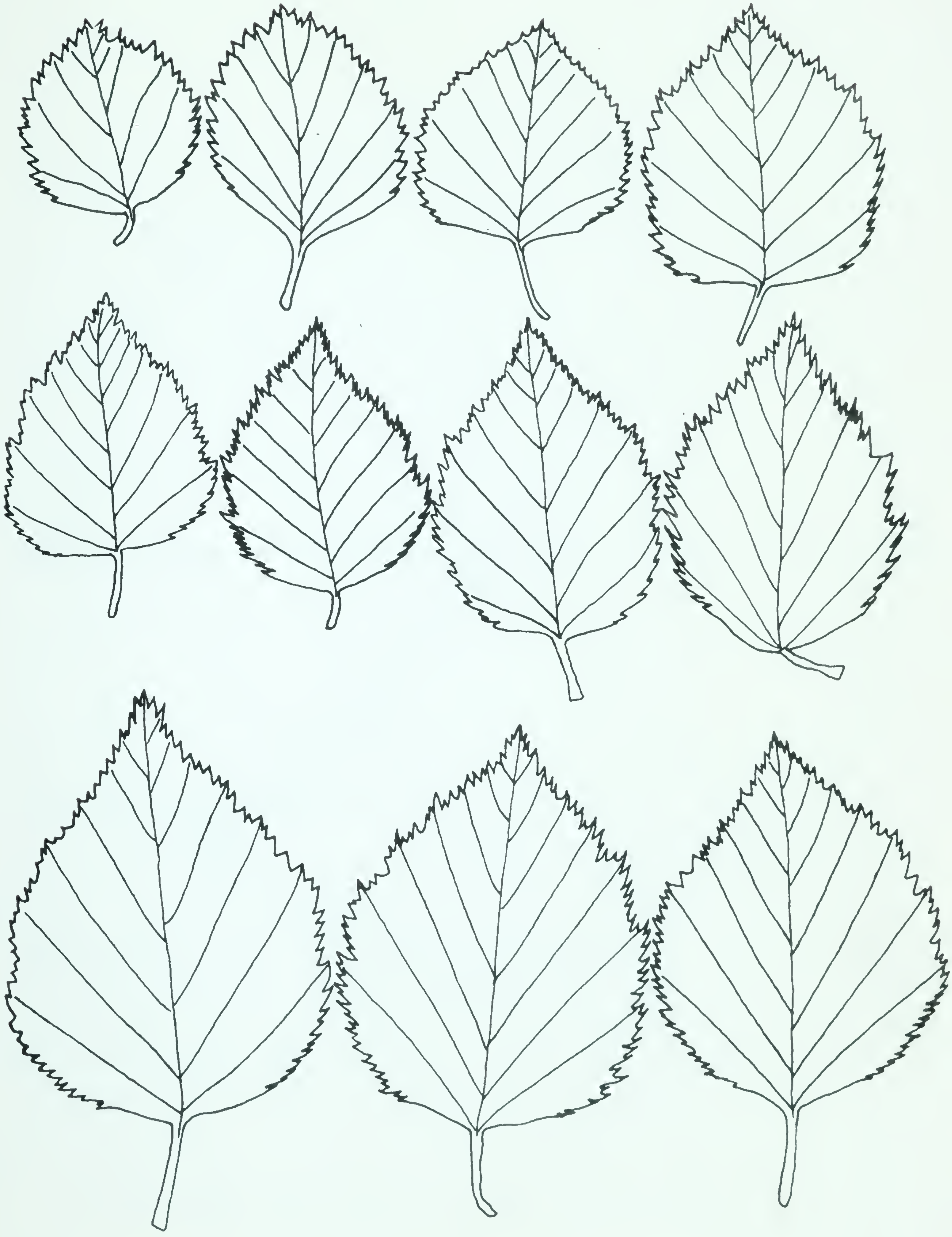
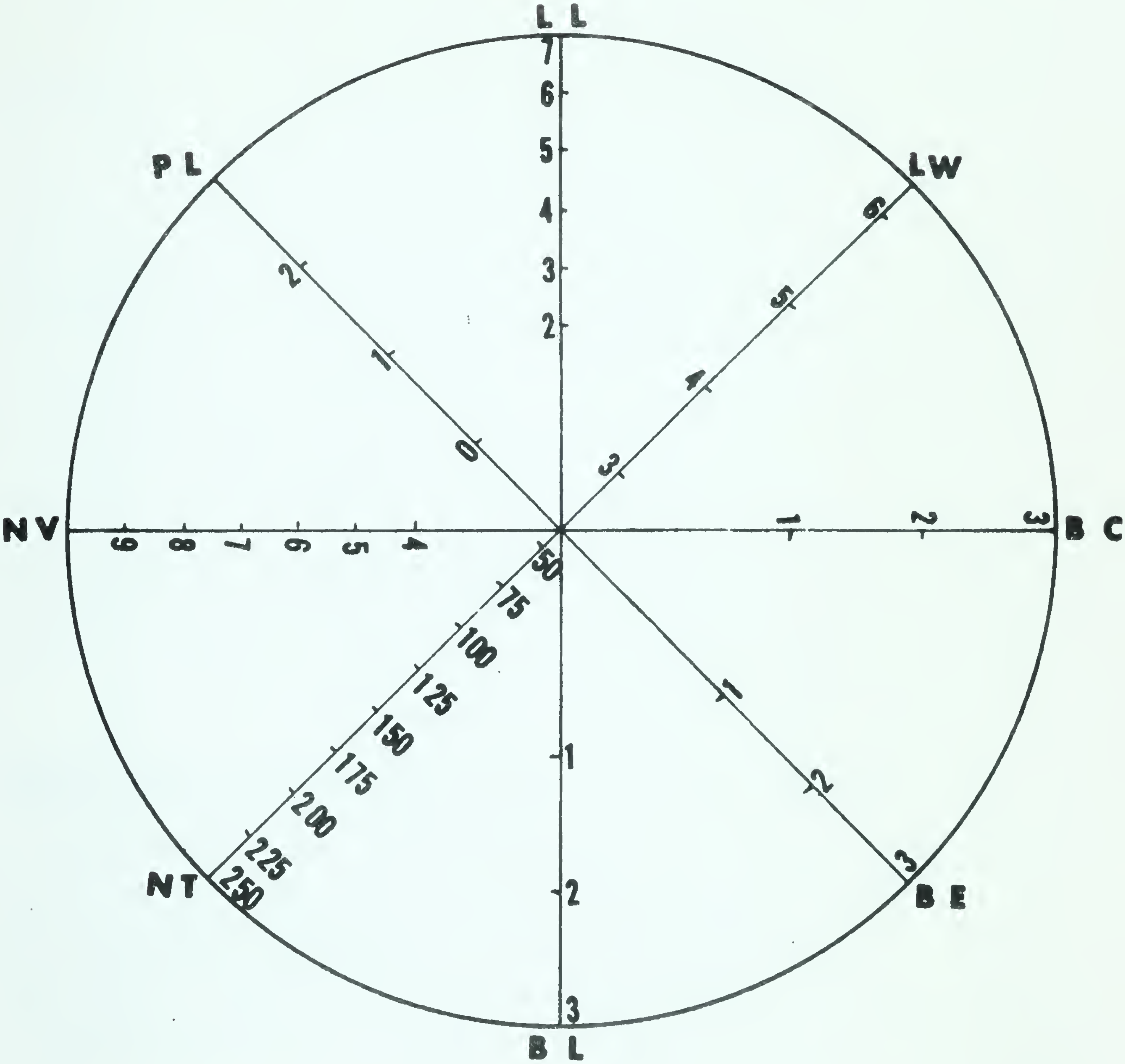


FIGURE a30

Key to the polygonal graphs of _Betula fontinalis_, _B. papyrifera_, and hybrids:

_LL_, leaf length in cm. _LW_, leaf width in cm. _BC_, bark color; 1 - brown, 2 - golden brown, 3 - beige-silver, white. _BE_, bark exfoliation; 1 - not exfoliating, 2 - partly exfoliating, 3 - exfoliating. _BL_, base of leaf; 1 - truncate, 2 - round, 3 - cuneate. _NT_, number of teeth on one margin of five leaves. _NV_, number of pairs of lateral leaf veins. _PL_, petiole length in cm.



L L
P L
L W
N V
B C
N T
B E
B L

FIGURE a31

Polygonal graphs of Betula fontinalis, B. papyrifera and hybrids.

The polygons are arranged to show successive increments in some characters from B. fontinalis through B. x utahensis to B. papyrifera. (See the following two pages).

Key

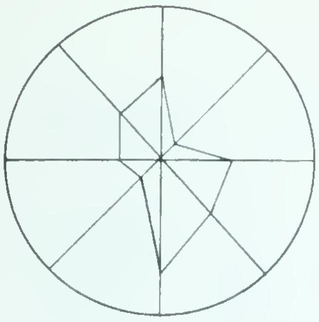
Sandberg 33 = Type specimen of B. utahensis Britton

Colo. 7 = From type tree of B. x andrewsii Nels.

Colo. 1 - 6 = Other material from B. x andrewsii population from Colorado.

Stokes April 18, 1900 = Type specimen of B. subcordata Rydb.

Butler 360 = Type specimen of B. montanensis Butler



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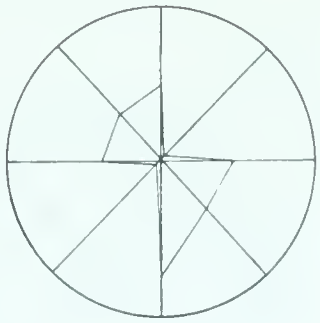
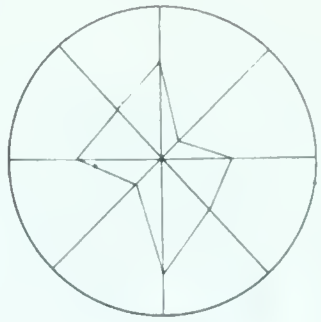


COLO.2



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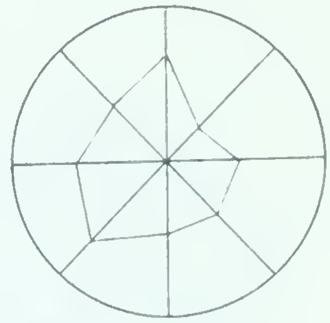

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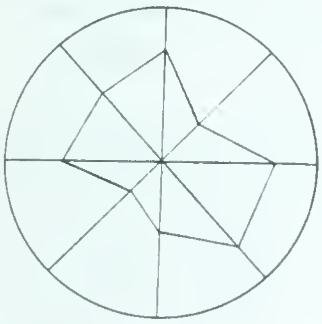
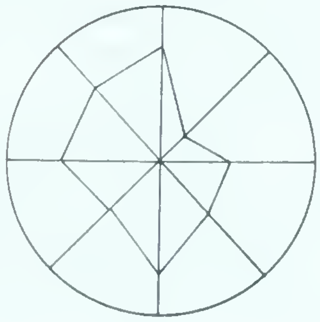
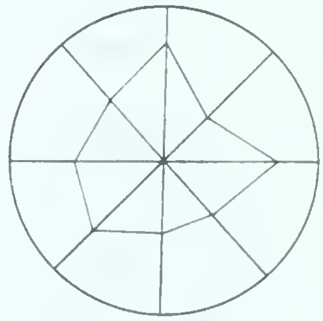


SANDBERG 33



COLO. 1



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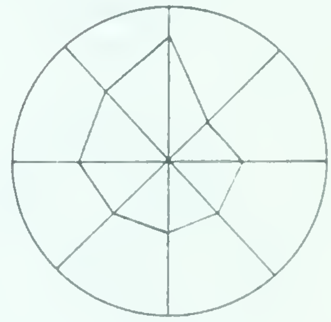

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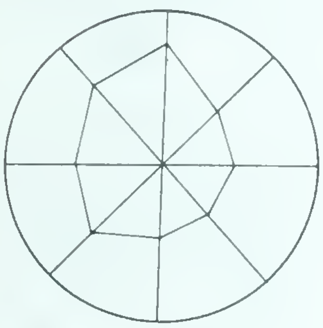

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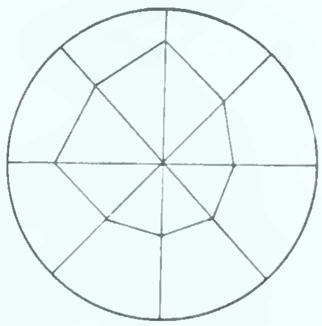

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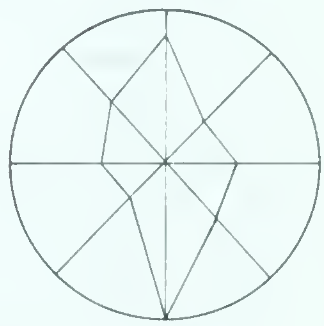

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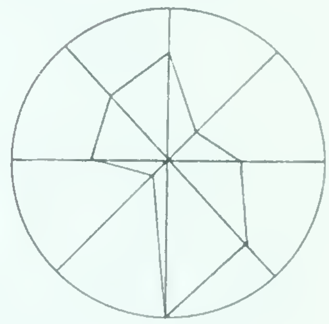
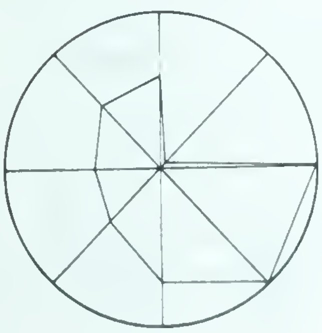


STOKES APRIL 18, 1900



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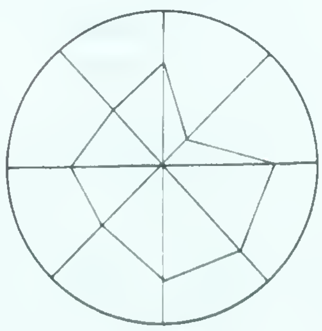

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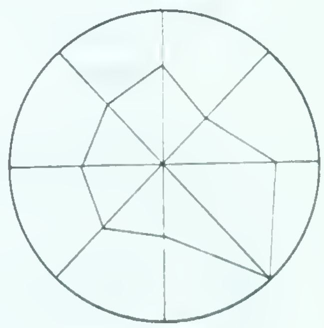

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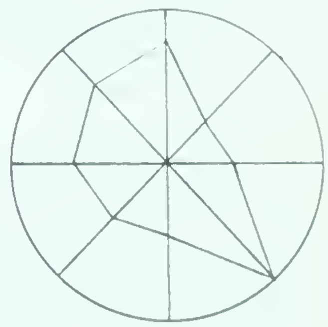
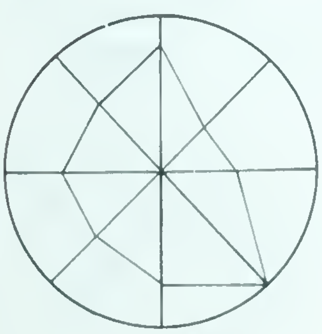


COLO.7



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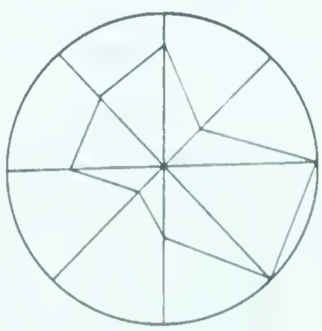

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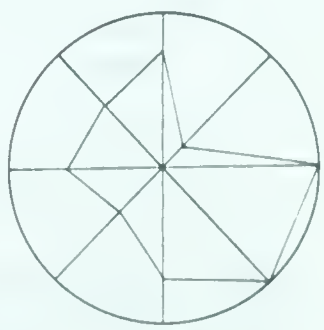

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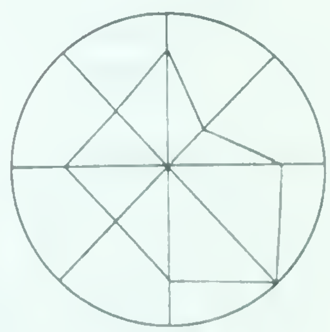

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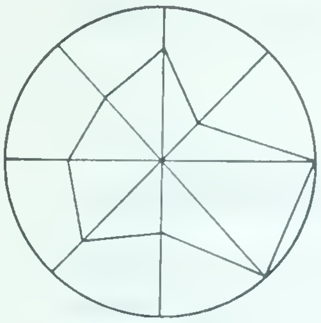
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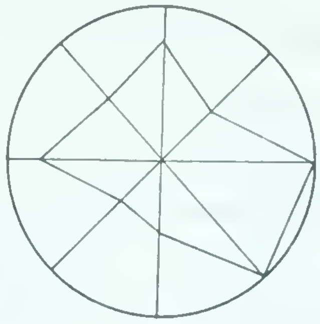
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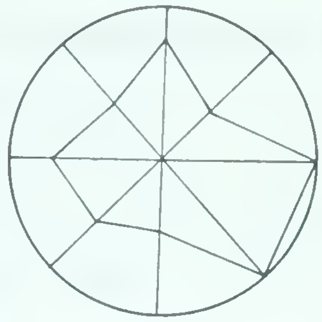
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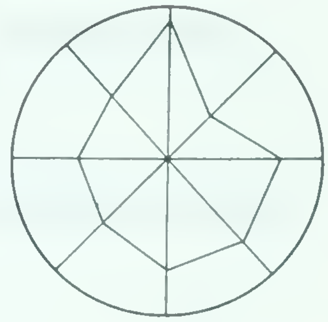
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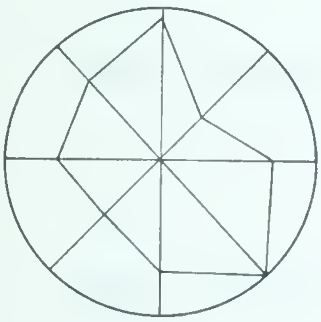
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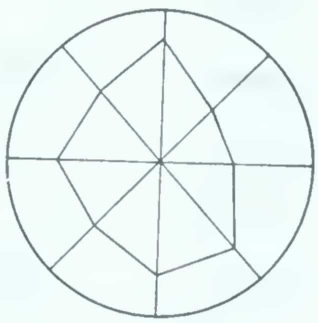
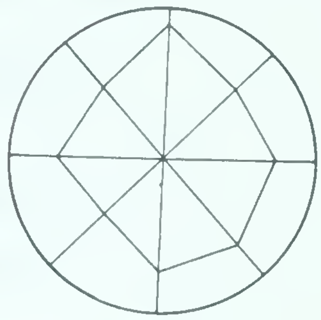

BUTLER 360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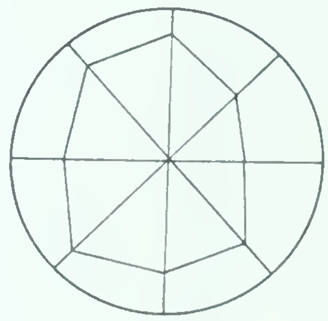
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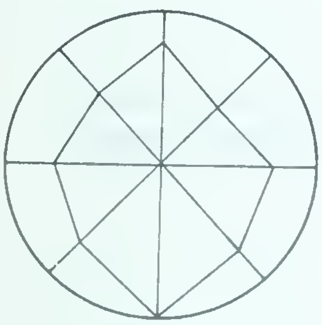
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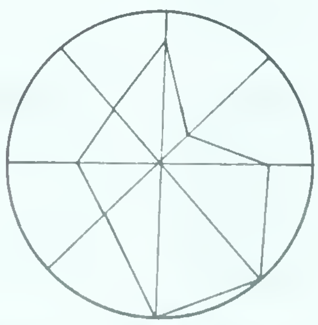
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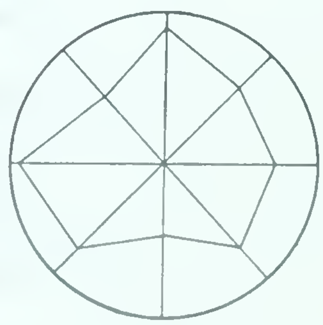
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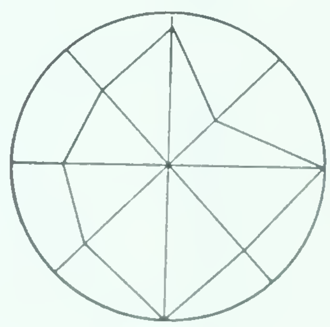
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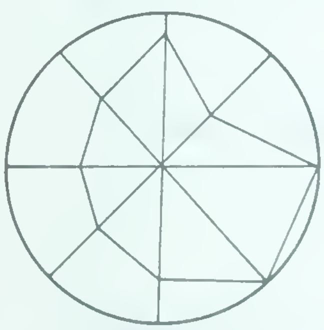
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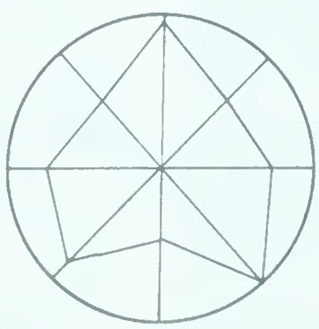
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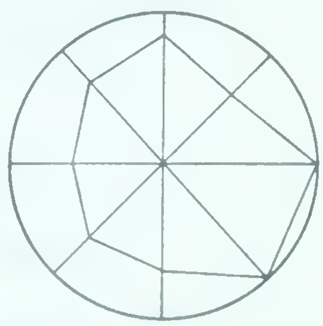
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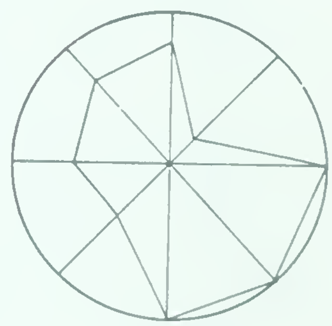
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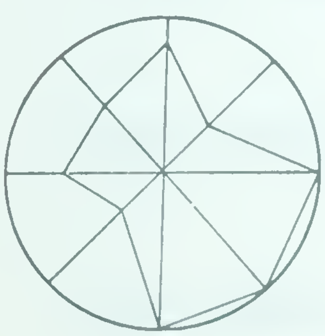
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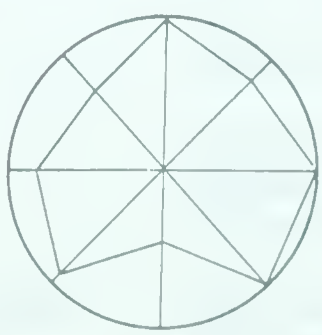
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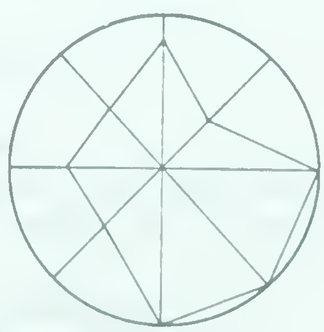
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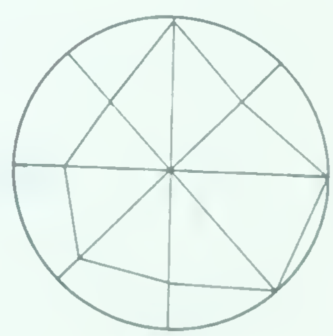
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TABLE a7

Hybrid index values of *Betula fontinalis*, *B. papyrifera* and hybrids.

Character	Range	Index number
Number of teeth on one side of five leaves	Less than 110	0
	110-160	1
	161-200	2
	More than 200	3
Leaf length (cm)	Less than 4	0
	4 - 5	1
	5.1-6	2
	More than 6	3
Leaf width (cm)	Less than 3	0
	3 - 4	1
	4.1 - 5	2
	More than 5	3
Pairs of lateral leaf veins	Less than 5.5	0
	5.5 - 6.5	1
	6.6 - 7.5	2
	7.6 - 8.5	3
	More than 8.5	4
Branchlet gland density	Glandular	0
	Slightly glandular	1
	Not glandular	2
Petiole length (cm)	Less than 1.1	0
	1.1 - 1.5	1
	1.6 - 2.0	2
	More than 2.0	3
Fruiting catkin length (cm)	Less than 2	0
	2 - 2.5	1
	2.6 - 3	2
	More than 3	3
Bark color	Dull brown	0
	Shiny brown to yellow-brown	1
	Silvery, gold to beige	2
Bark exfoliation	Non-exfoliating	0
	Slightly exfoliating	1
	Exfoliating	2

TABLE a8

Celestine Lake birches, summary of morphological data.

Collection number	Stomatal size (μ)	Number of stems	Hybrid index
1929	27.8	6	17
1930	23.1	3	15
1931	28.2	2	21
1932	24.9	4	16
1933	-	6	22
1934	-	3	19
1935	-	several	4
1936	-	several	2
1937	-	several	3
1938	-	several	2
1939	-	several	4
1940	31.2	2	18
1941	23.9	5	19
1942	24.8	5	20
1943	25.4	3	16
1944	27.2	6	19
1945	24.8	3	16
1946	27.4	3	13
1947	25.6	7	12
1948	24.5	2	14

FIGURE a32

Leaf tracings of Betula x sargentii, B. papyrifera and hybrids.

Leaves in the first row, upper left are B. x sargentii while those in the third row are B. papyrifera. Those between are hybrids.

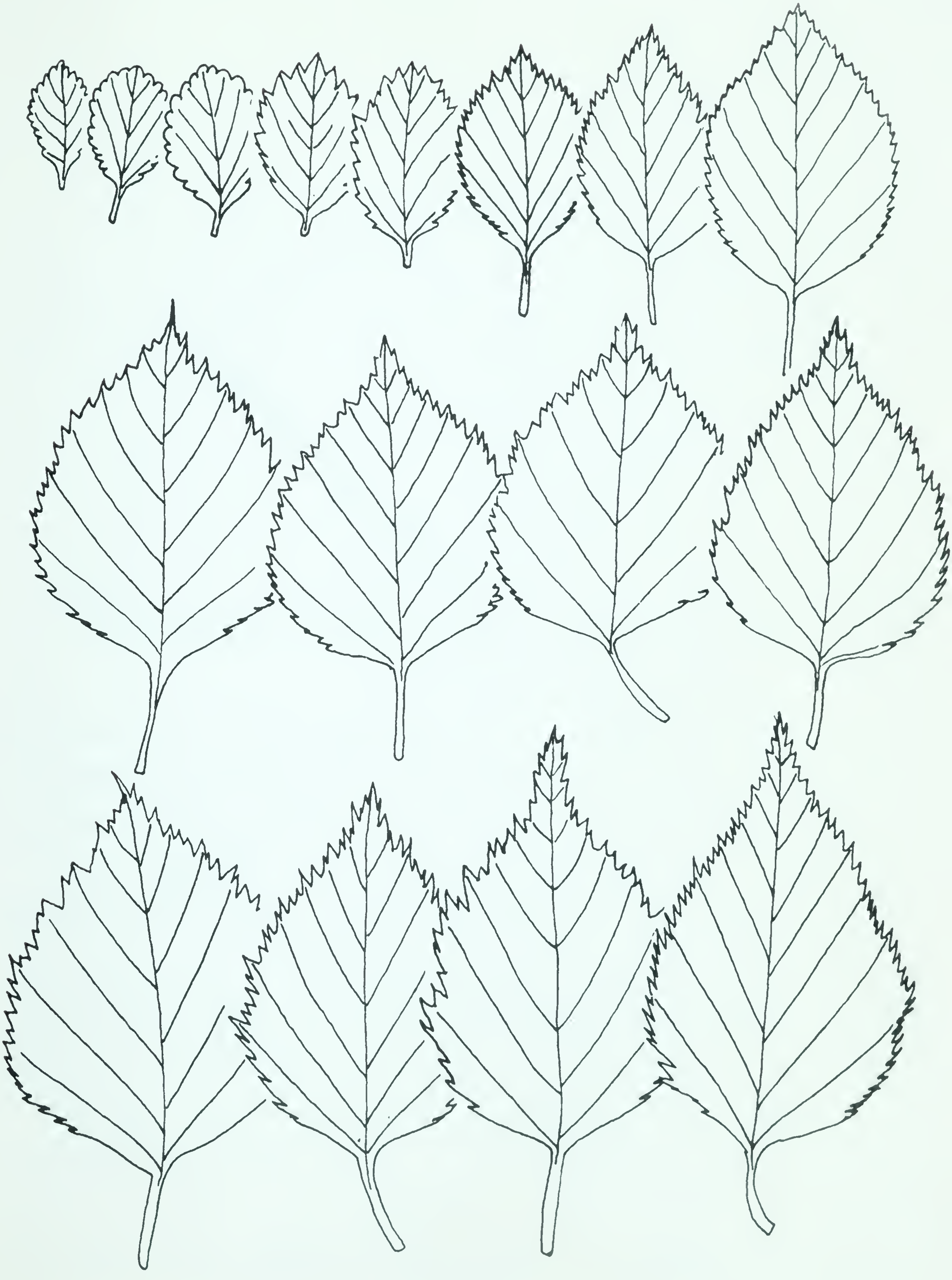
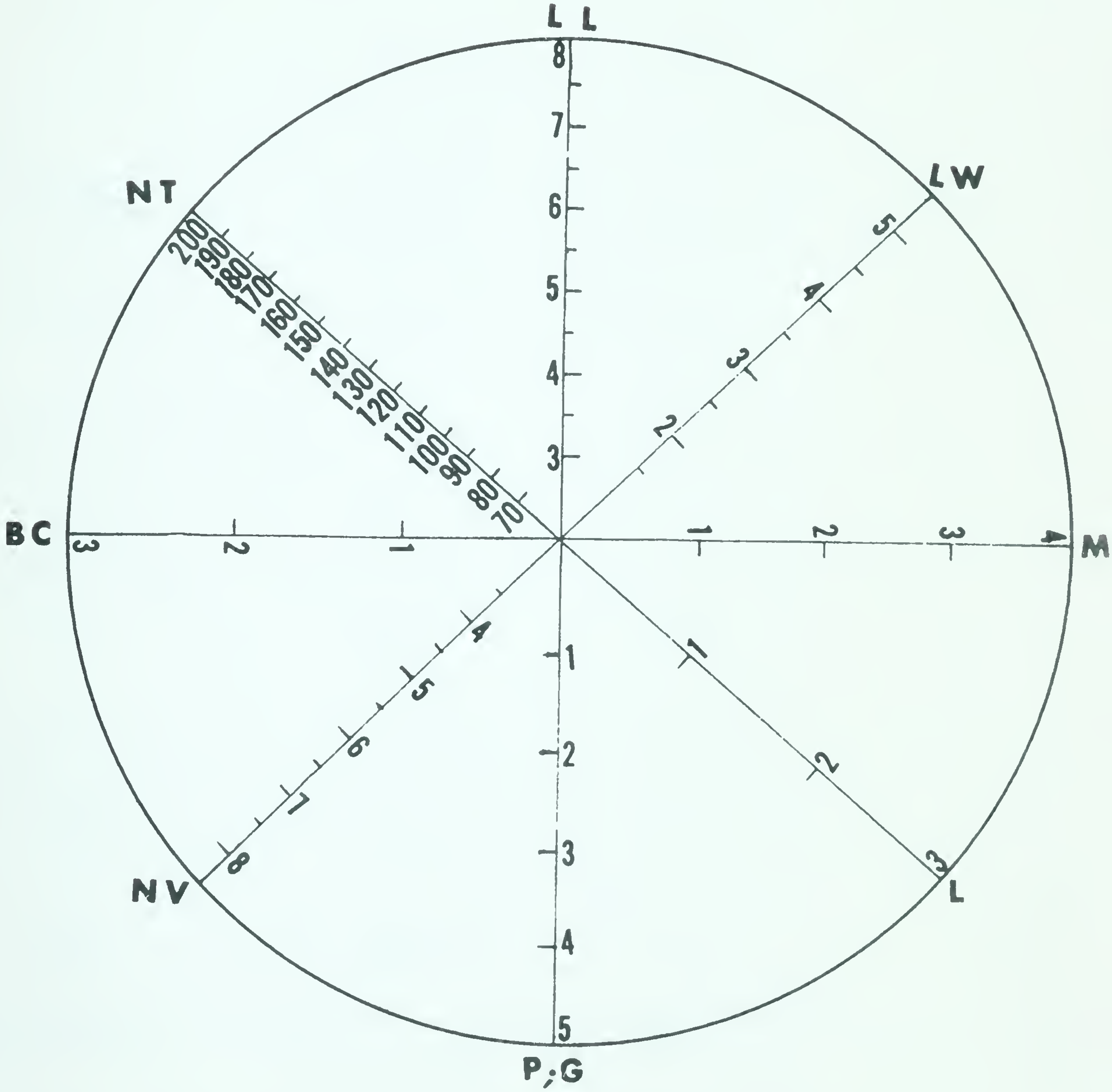


FIGURE a33

Key to polygonal graphs of _Betula_ x _sargentii_, _B._ _papyrifera_ and hybrids:

_LL_, leaf length in cm. _LW_, leaf width in cm. _M_, margin of leaf; 1 - crenate-serrate, 2 - serrate, 3 - partly doubly-serrate, 4 - doubly-serrate. _L_, leaf lobing; 1 - not lobed, 2 - slightly lobed, 3 - lobed. _P;G_, pubescence of leaves and glandular condition of branchlets; 1 - no pubescence, glandular, 2 - no pubescence, slightly glandular, 3 - pubescent, slightly glandular, 4 - no pubescence, no glands, 5 - pubescent, no glands. _NV_, number of pairs of lateral leaf veins. _BC_, bark color and exfoliation; 1 - brown and non-exfoliating, 2 - brown to gray and exfoliating, 3 - white to cream and exfoliating. _NT_, number of teeth on one side of five leaves.

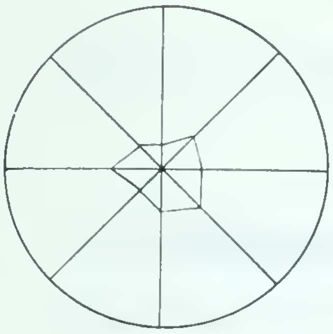


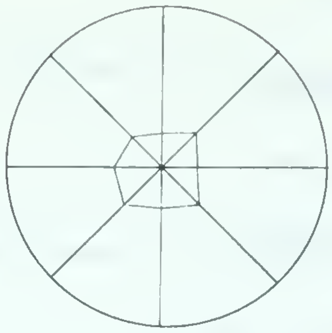
L L
LW
M
L
P;G
NV
BC
NT
200
190
180
170
160
150
140
130
120
110
100
90
80
70

FIGURE a34

Polygonal graphs of *Betula* x *sargentii*, *B*. *papyrifera* and hybrids.

The polygons are arranged to show successive increments in some characters from *B*. x *sargentii* through *B*. x *arbuscula* to *B*. *papyrifera*.


1912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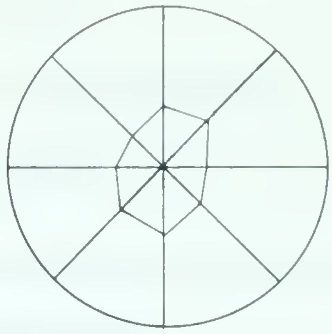
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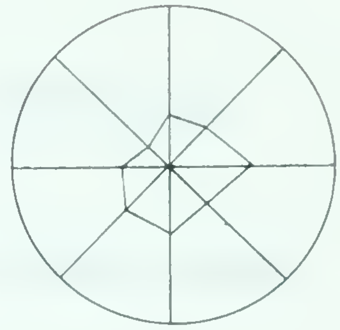
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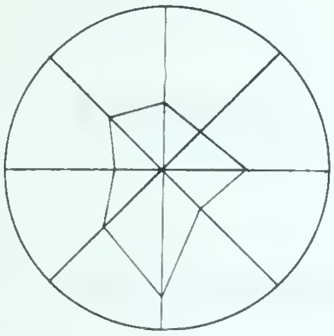
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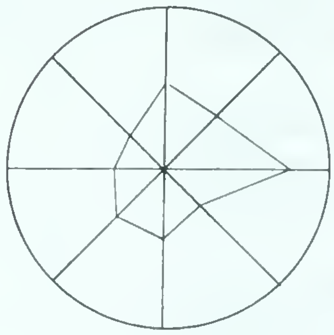
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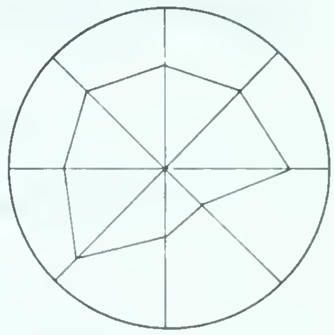
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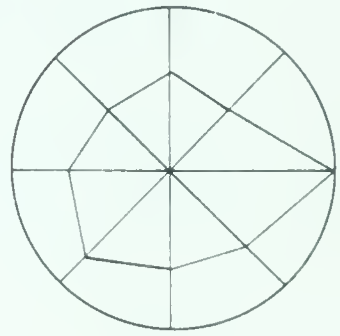
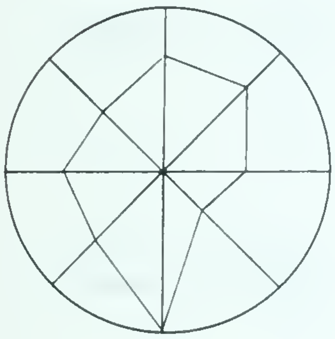
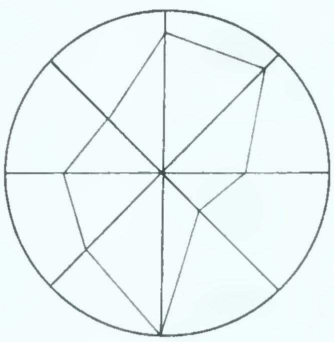
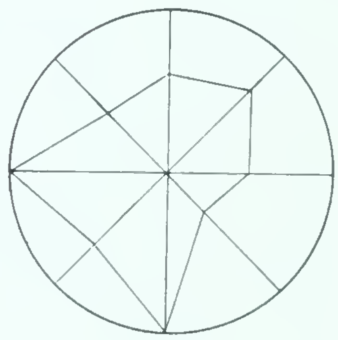

2257


1738


2241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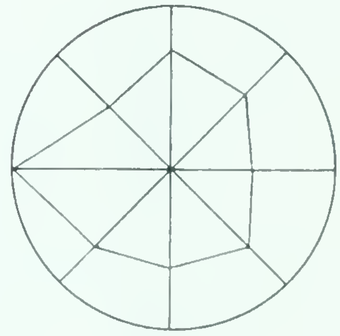
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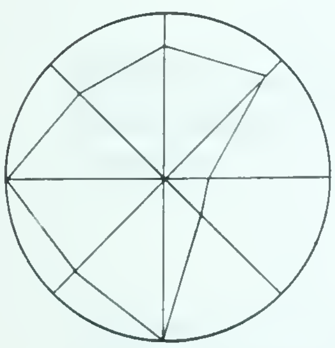
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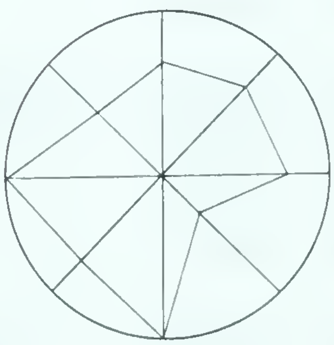
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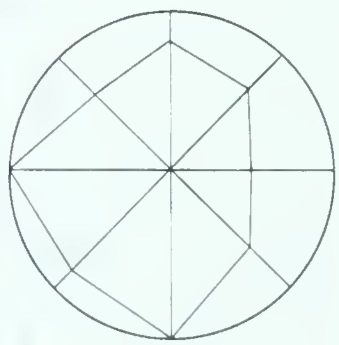
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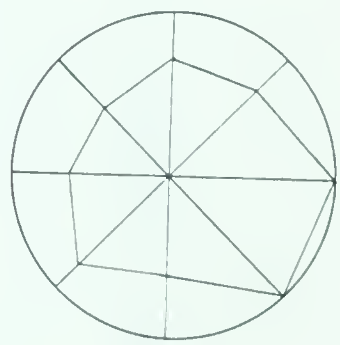
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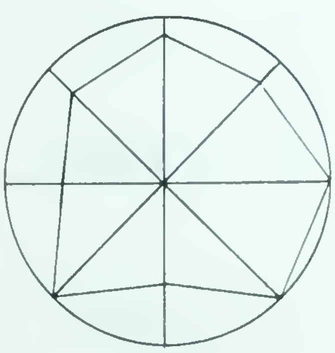
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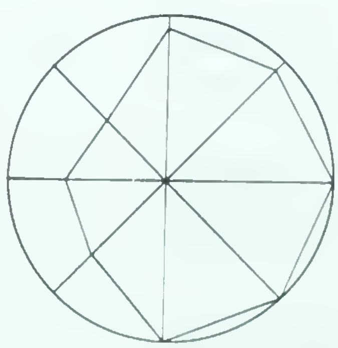
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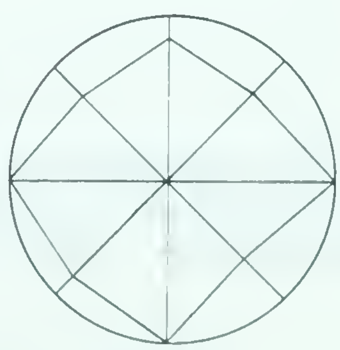
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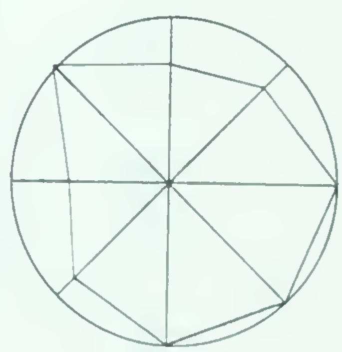

1749

TABLE a9

Hybrid index values of Betula x sargentii, B. papyrifera and hybrids.

Character	Range	Index number
Leaf margin	Crenate-serrate	0
	Serrate	1
	Partly doubly-serrate	2
	Doubly-serrate	3
Leaf tip	Round acute	0
	Acute	1
	Acute-acuminate	2
Leaf lobing	Not lobed	0
	Slightly lobed	1
	Lobed	2
Leaf length (cm)	Less than 3	0
	3 - 4	1
	4.1 - 5	2
	5.1 - 6	3
	More than 6	4
Leaf width (cm)	Less than 2	0
	2 - 3	1
	3.1 - 4	2
	More than 4	3
Number of teeth on one side of five leaves	Less than 70	0
	70 - 110	1
	111 - 130	2
	131 - 150	3
	More than 150	4
Pairs of lateral leaf veins	Less than 4	0
	4 - 5	1
	5.1 - 6	2
	6.1 - 7	3
	More than 7	4
Bark	Brown and non-exfoliating	0
	Brown to gray, exfoliating	1
	White to cream, exfoliating	2
Branchlets	Glandular	0
	Slightly glandular	1
	Not glandular	2

TABLE a10

Hybrid index values of the birches analyzed in the Jasper collections of *Betula* x *sargentii*, *B. papyrifera*, and *B.* x *arbuscula*.

Collection number	Hybrid index
1902	0
1910	0
1916	0
1912	1
1914	1
2245	1
1923	2
1922	3
1924	3
1732	5
1736	6
1920	6
1734; 2240	9
1748	11
1738	15
1743	15
2241	17
1750	18
1733	18
2256	19
2257	19
1765	20
1746	21
1767	21
1736	22
1747	22
1735	22
1745	24
1768	24
1737	25
1744	25
1749	25
1766	25

TABLE all

Frequency distribution of mean stomatal length (μ) in

Betula papyrifera, B. x sargentii, and hybrid populations

(Jasper collection areas)

Size class (μ)	Number of individuals		
	Betula x sargentii	B. x arbuscula	B. papyrifera
18.1 - 20.0	3	-	-
20.1 - 22.0	2	-	-
22.1 - 24.0	2	1	-
24.1 - 26.0	1	1	-
26.1 - 28.0	-	1	1
28.1 - 30.0	-	5	1
30.1 - 32.0	-	2	-
32.1 - 34.0	-	2	3
34.1 - 36.0	-	2	1
More than 36.0	-	1	-
Total	8	15	5

FIGURE a35

Leaf tracings of _Betula resinifera_, _B. papyrifera_ and hybrids.

Leaves in the first row are _B. resinifera_, those in the last row are _B. papyrifera_ and those between are hybrids.

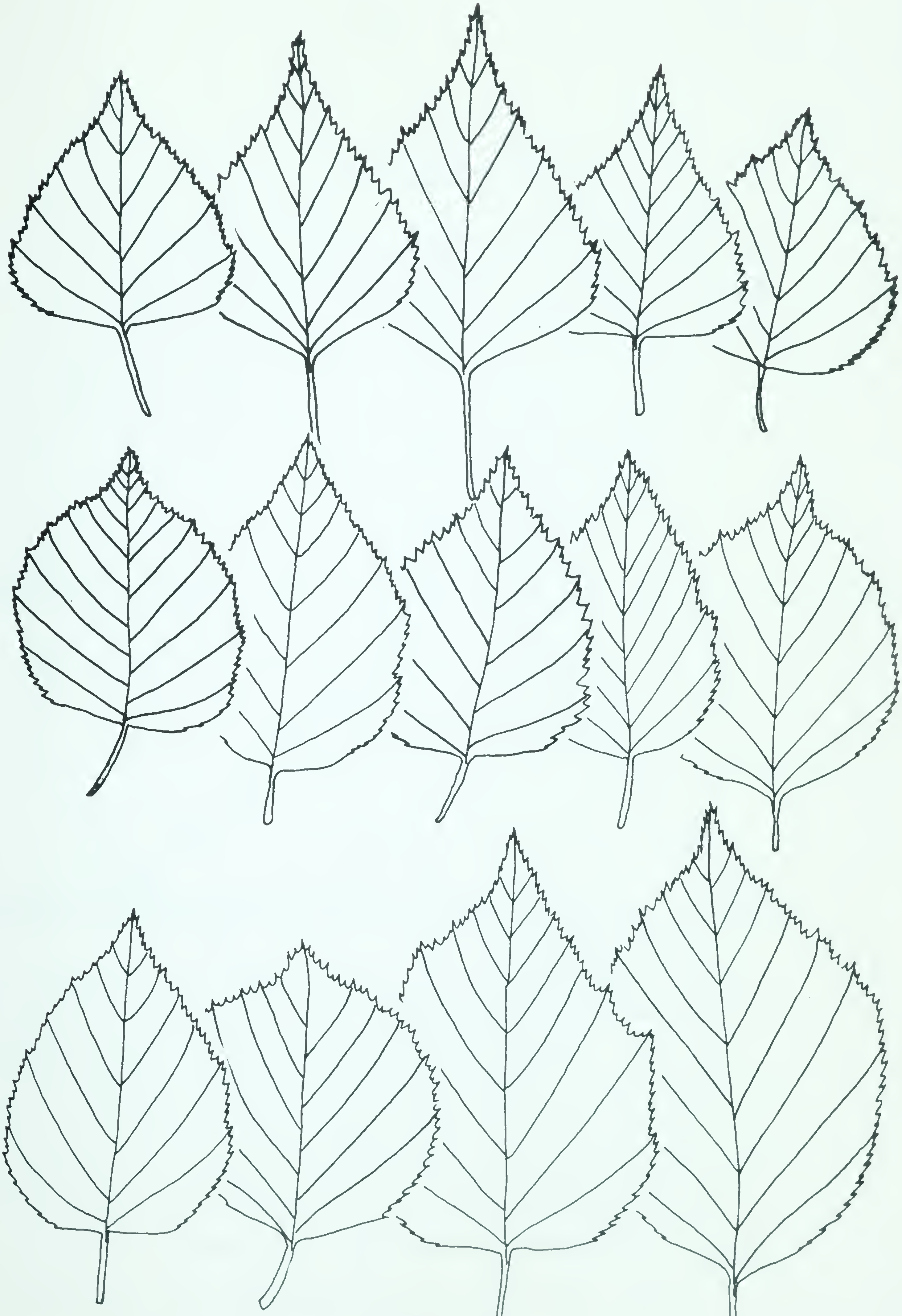
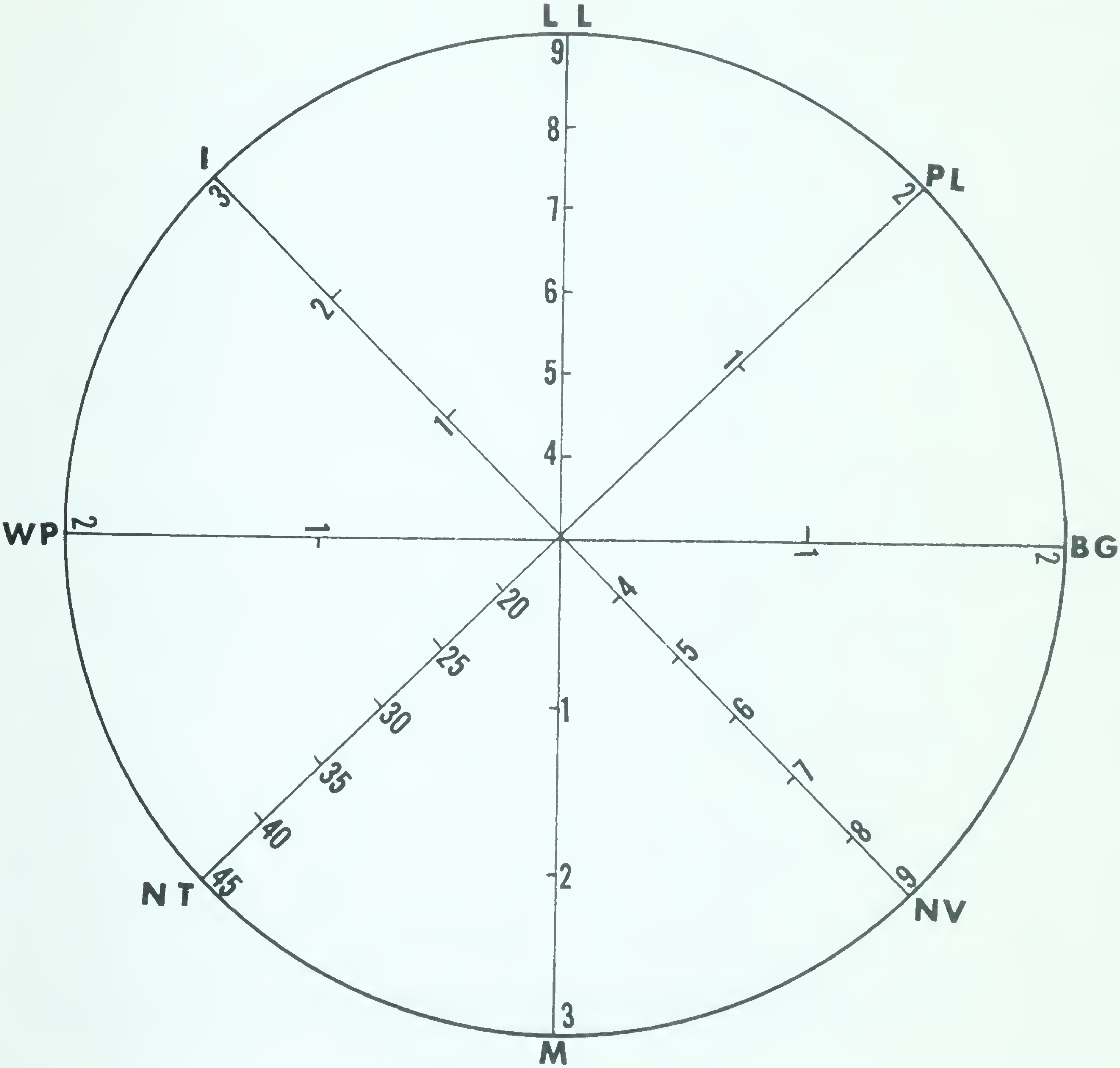


FIGURE a36

Key to polygonal graphs of *Betula resinifera*, *B. papyrifera*, and hybrids:

LL, leaf length in cm. *PL*, leaf pubescence; 1 - glabrous below, 2 - pubescen in vein axils below. *BG*, branchlet glands; 1 - present, 2 - absent. *NV*, number of pairs of lateral leaf veins. *M*, margin of leaf; 1 - serrate, 2 - partly doubly-serrate, 3 - doubly-serrate. *NT*, number of teeth on one side of one leaf. *WP*, widest point on leaf; 1 - below mid-point, 2 - at mid-point. *I*, impression; 1 - *B. resinifera*, 2 - hybrid, 3 - *B. papyrifera*.

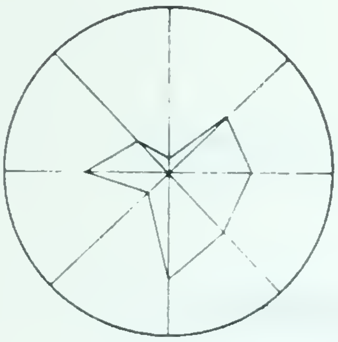


L L
9
8
7
6
5
4
I
3
2
1
PL
2
1
WP
2
1
BG
1
2
20
25
30
35
40
45
N T
4
5
6
7
8
9
NV
1
2
3
M

FIGURE a37

Polygonal graphs of *Betula resinifera*, *B. papyrifera* and hybrids.

The polygons are arranged to show successive increments in some characters from *B. resinifera* through *B. x winteri* to *B. papyrifera*.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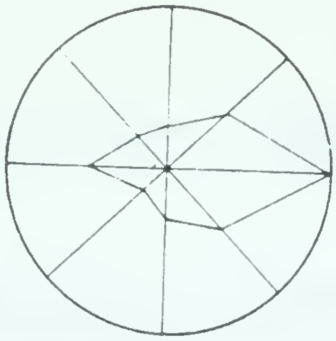
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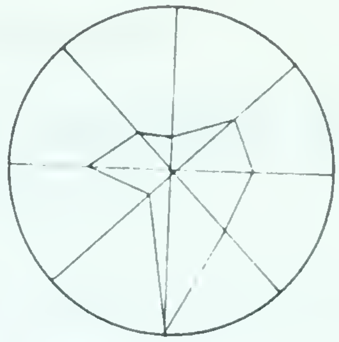
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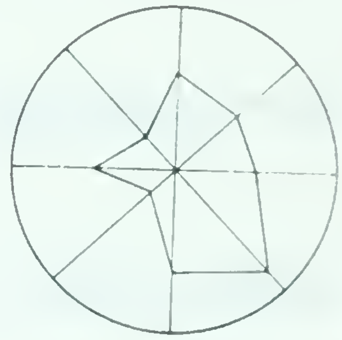
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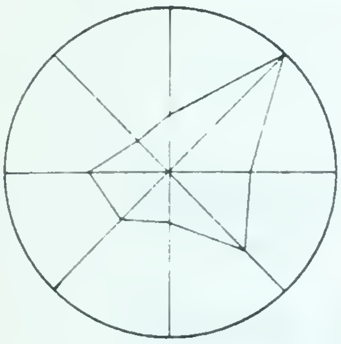
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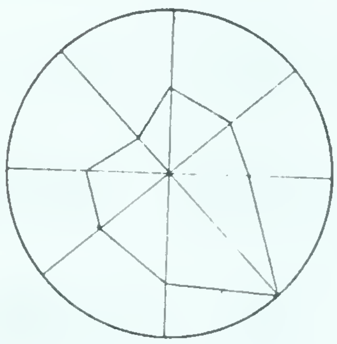
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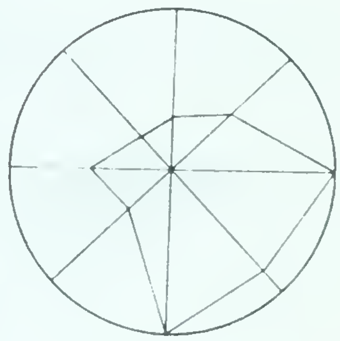
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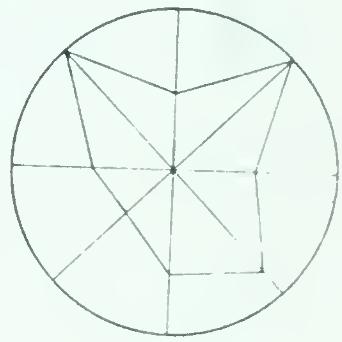
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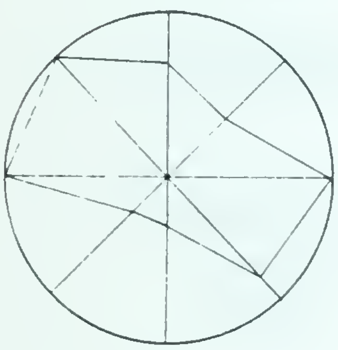
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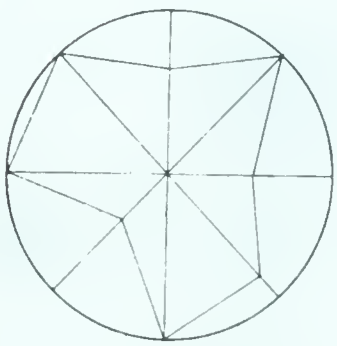
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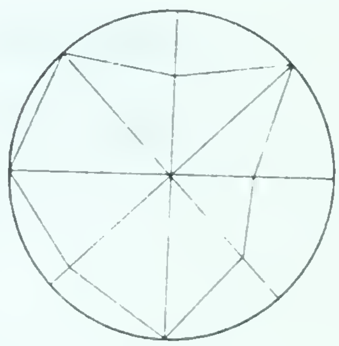
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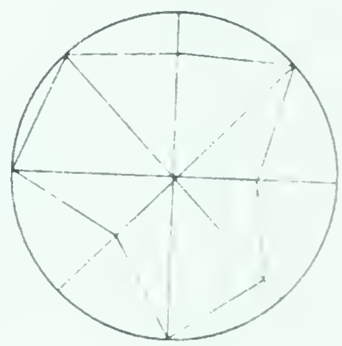
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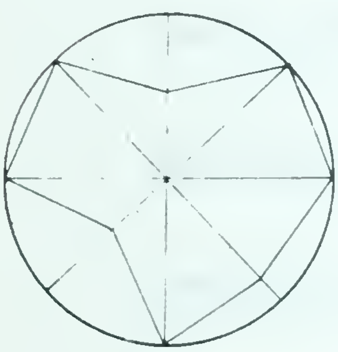
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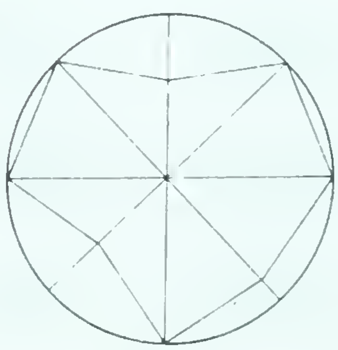
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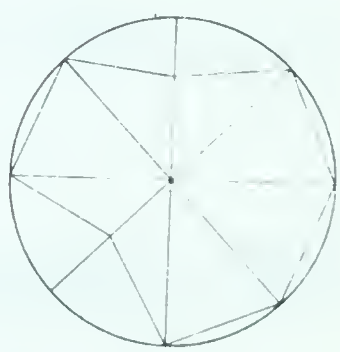
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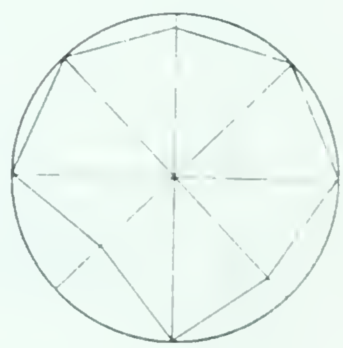
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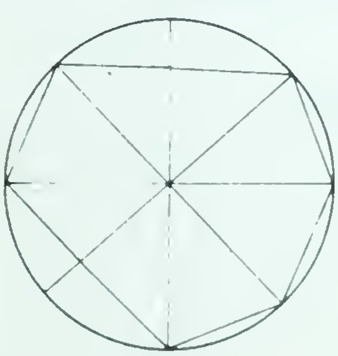
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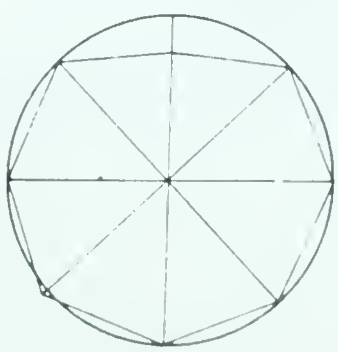
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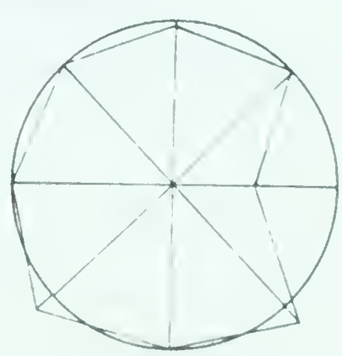
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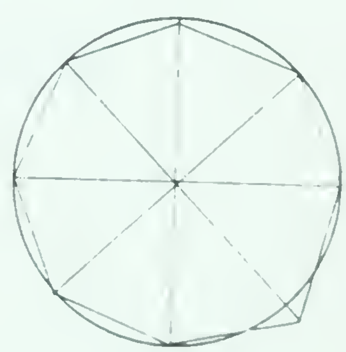

1812

TABLE a12

Hybrid index values of *Betula papyrifera*, *B. resinifera*, and hybrids.

Character	Range	Index number
Leaf length (cm)	Less than 4.5	0
	4.6 - 5.5	1
	5.6 - 6.5	2
	6.6 - 7.5	3
	More than 7.5	4
Widest point of leaf	Below the mid-point	0
	At the mid-point	2
Number of teeth on one side of one leaf	Less than 27	0
	28 - 35	1
	More than 35	2
Impression	*Betula resinifera*	0
	Hybrid	1
	Betula papyrifera	2
Number of pairs of lateral leaf veins	Less than 6	0
	6.1 - 7	1
	7.1 - 8	2
	8.1 - 9	3
	More than 9	4
Leaf epidermis	Glabrous below	0
	Pubescent in axils below	2
Branchlet glands	Present	0
	Absent	2
Margin of leaf	Serrate or partly doubly-serrate	0
	Doubly-serrate	1
Leaf tip	Acuminate	0
	Short-acuminate	1

TABLE a13

Frequency distribution of mean stomatal lengths (μ) in *Betula resinifera*, *B. papyrifera* and hybrids.

Size class (μ)	Number of individuals		
	Betula resinifera	B. x winteri	B. papyrifera
15.1-17.0	1	-	-
17.1-19.0	2	1	-
19.1-21.0	1	2	-
21.1-23.0	-	2	4
23.1-25.0	2	4	2
25.1-27.0	-	7	5
27.1-29.0	-	5	4
29.1-31.0	-	5	1
31.1-33.0	-	5	2
33.1-35.0	-	1	1
35.1-37.0	-	-	-
37.1-39.0	-	1	1
Total	6	33	20

TABLE a14

Chromosome numbers of *Betula resinifera*, *B. papyrifera*, and *B.* x *winteri*

Taxon	Collection number	Chromosome number
B. resinifera	1414, 1427, 1443, 1447, 1475, 1501, 1502, 1506, 1521, 1522, 1524, 1528, 1530, 1531, 1540, 1551, 1552, 1553, 1560, 1561, 1571, 1572, 1573, 1578, 1579, 1608, 1609, 1610, 1614, 1616, 1617, 1618, 1619, 1696, 1716	2n = 28
	2155, 2156, 2181	n = 14
B. papyrifera	2257	n = 28
	1574, 1743	2n = c 56
	1677	2n = c 62
	1588	2n = c 63
	1638	2n = c 64
	1669	2n = c 68
	1639	2n = c 72
	1666	2n = c 74
	1667, 1662	2n = c 75
	1767	2n = c 77
	1679	2n = 78
	1665	2n = c 79
	1640	2n = c 80

Table a14, continued

Taxon	Collection number	Chromosome number
B. papyrifera	1661, 1678, 1765, 1664	2n = 84
	1694, 1695	n = 42
B. x winteri	2134	2n = 28
	1477, 1576, 1490, 1580	2n = c 35
	1586, 1368	2n = 56
	1587, 1589, 1811	2n = c 56
	1596	2n = c 65
	1585	n = 35; 2n = 70
	1590	2n = 84

FIGURE a38

Leaf tracings of Betula pumila var. glandulifera, B. papyrifera and hybrids.

Leaves in the first row, upper left are B. pumila var. glandulifera, those in the last row are B. papyrifera and those between are hybrids.

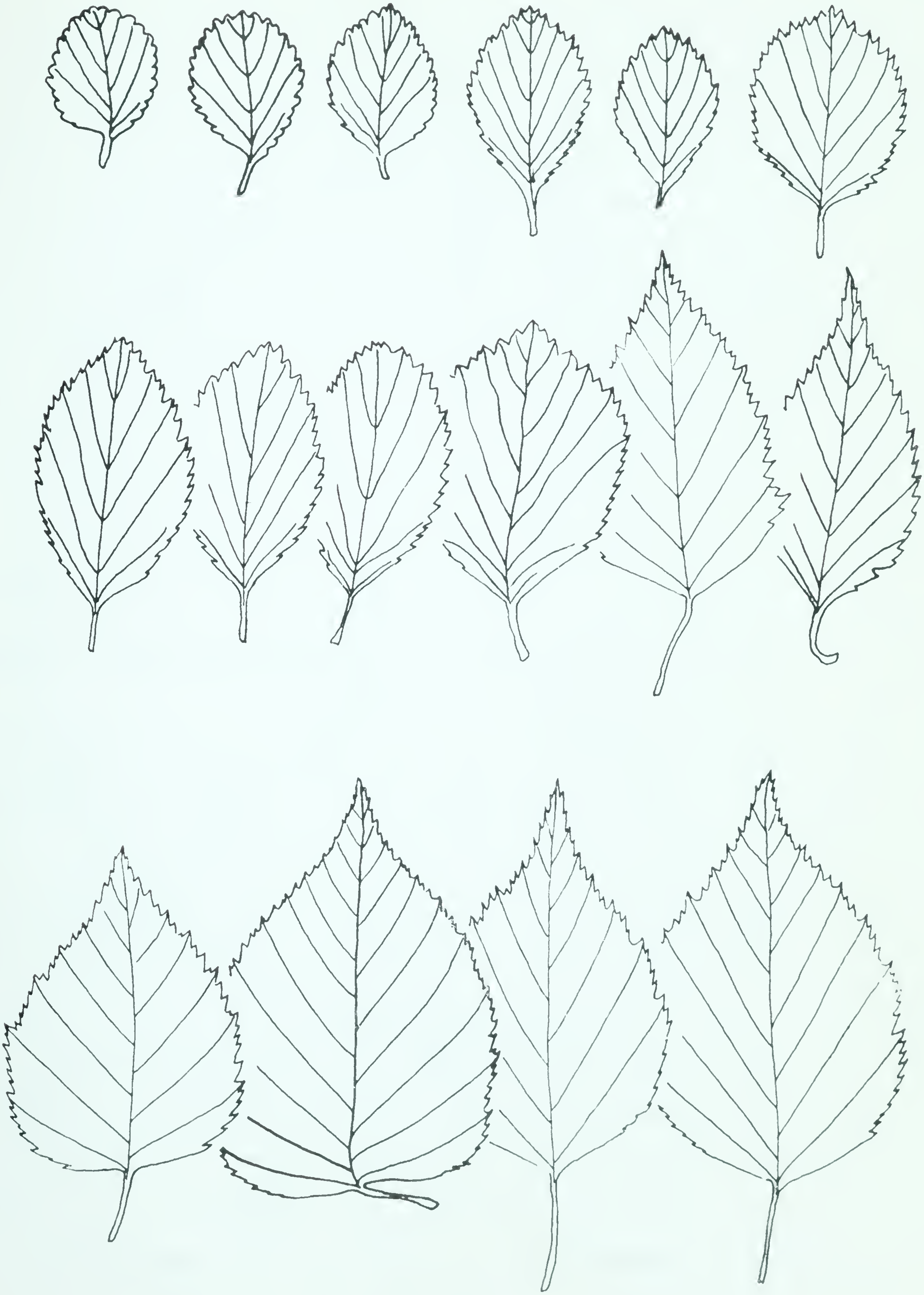
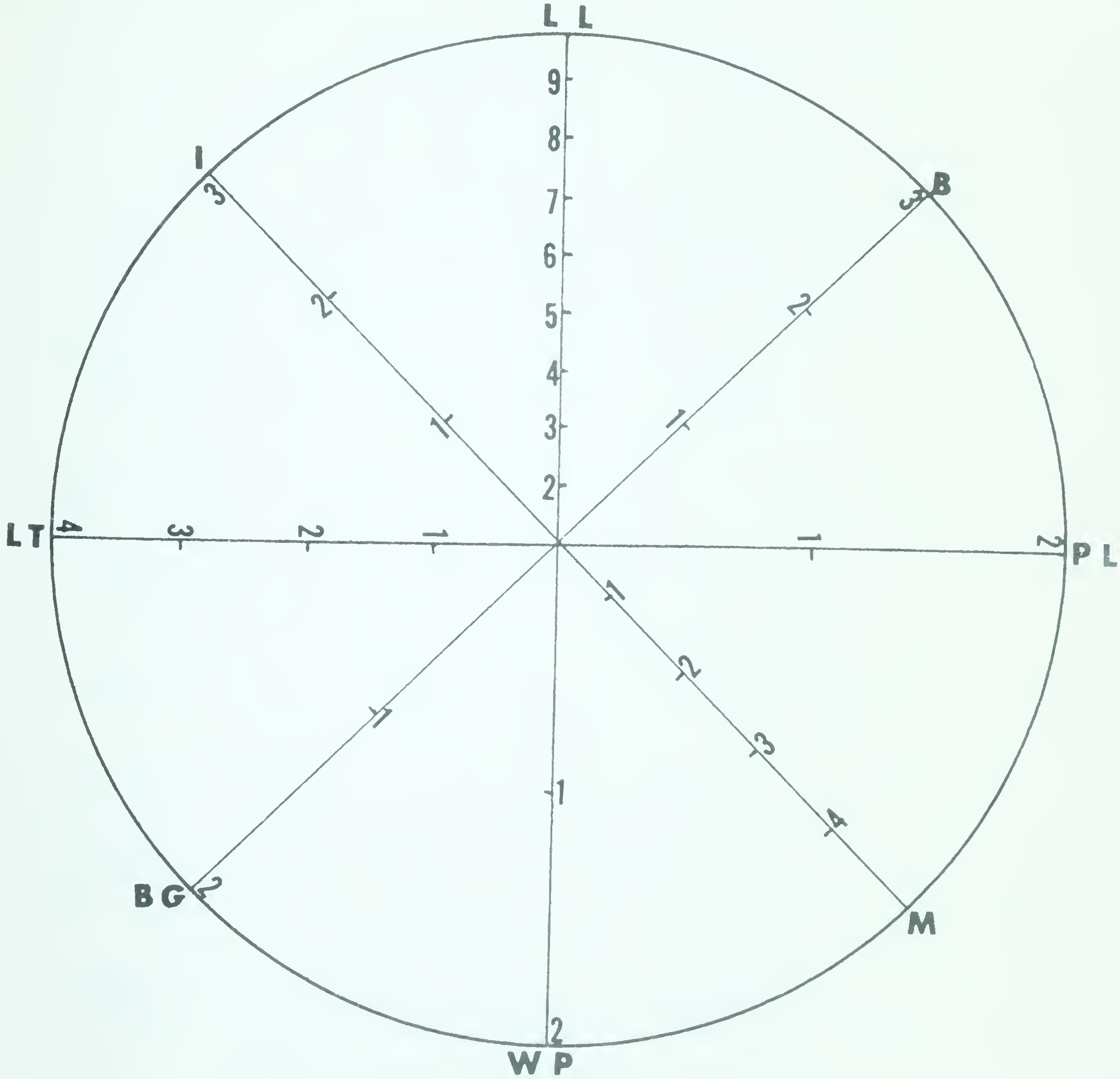


FIGURE a39

Key to polygonal graphs of *Betula papyrifera*, *B. pumila* var. *glandulifera* and hybrids:

LL, leaf length (cm). *B*, bark color and exfoliation; 1 - brown and non-exfoliating, 2 - dark and exfoliating, 3 - light and exfoliating. *LP*, leaf pubescence; 1 - glabrous below, 2 - pubescent in vein axils below. *M*, margin of leaf; 1 - crenate, 2 - crenate-serrate, 3 - serrate, 4 - partly doubly-serrate, 5 - doubly-serrate. *WP*, widest point on leaf; 1 - above the mid-point, 2 - at the mid-point. *BG*, branchlet glands; 1 - present, 2 - absent. *LT*, leaf tip; 1 - round, 2 - round-acute, 3 - acute, 4 - acuminate. *I*, impression; 1 - *B. pumila* var. *glandulifera*, 2 - hybrid, 3 - *B. papyrifera*.

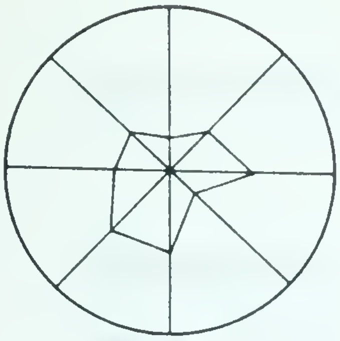


L L
I
B
LT
P L
B G
M
W P

FIGURE a40

Polygonal graphs of _Betula papyrifera_, _B_. _pumila_ var. _glandulifera_ and hybrids.

The polygons are arranged to show successive increments in some characters from _B_. _pumila_ var. _glandulifera_ through _B_. x _sandbergii_ to _B_. _papyrifera_.



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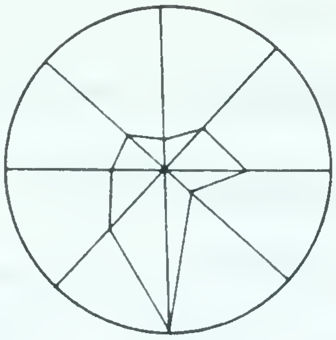

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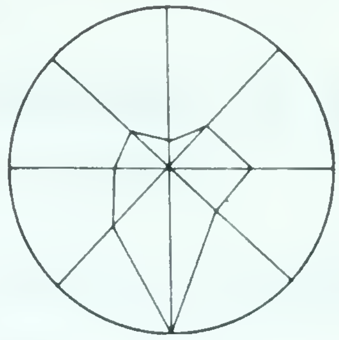

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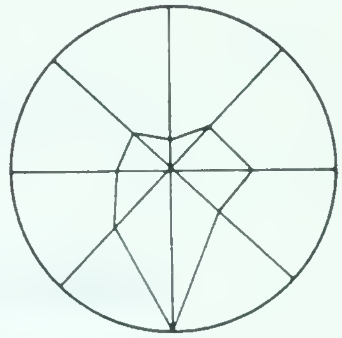

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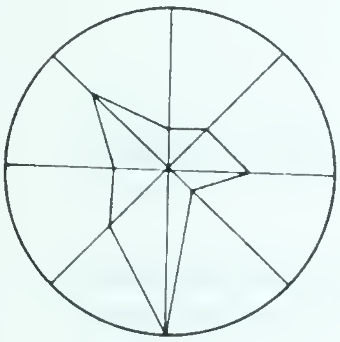
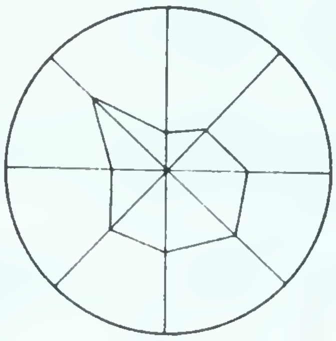


2149



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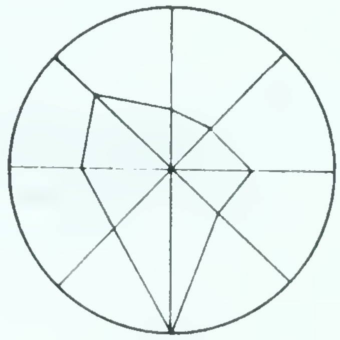

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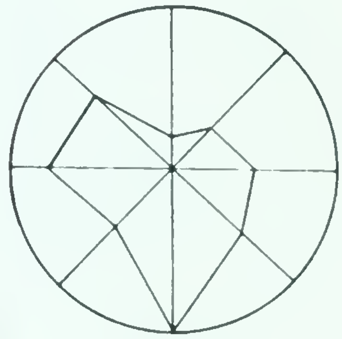

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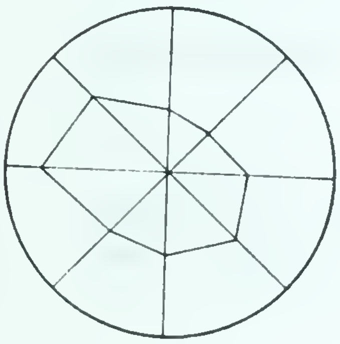

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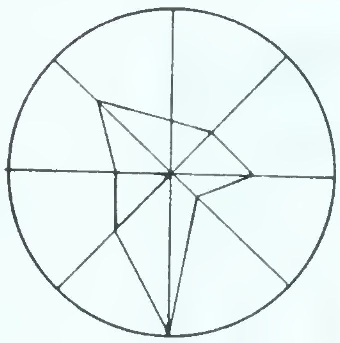

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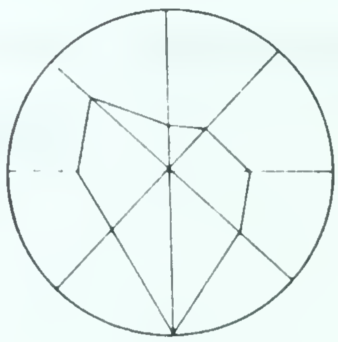

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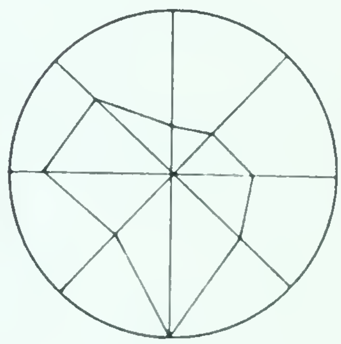

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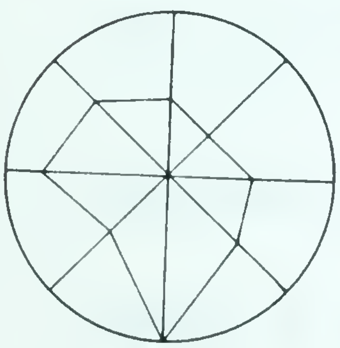

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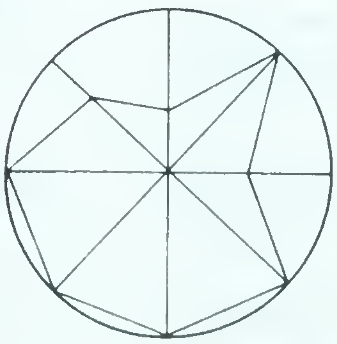

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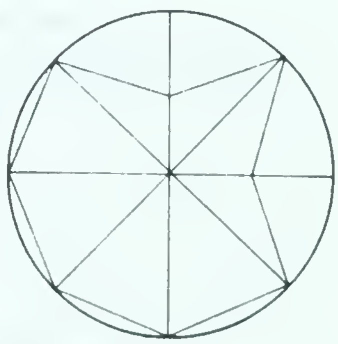

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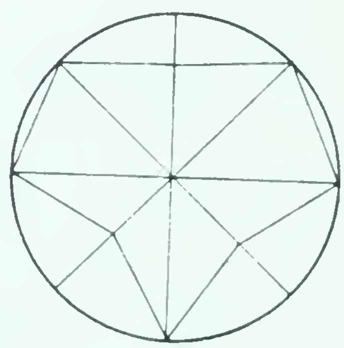

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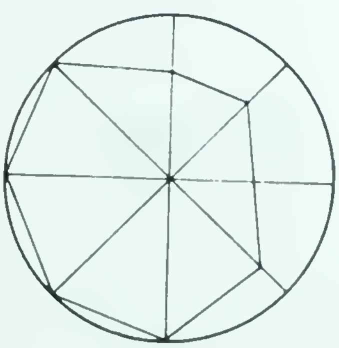

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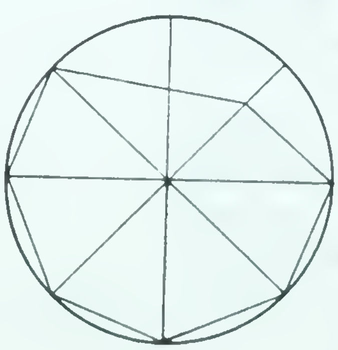

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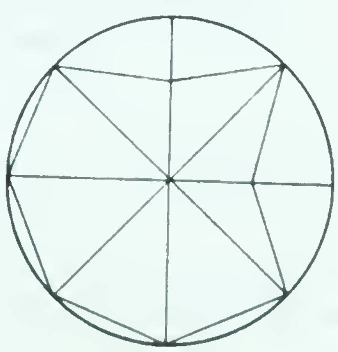

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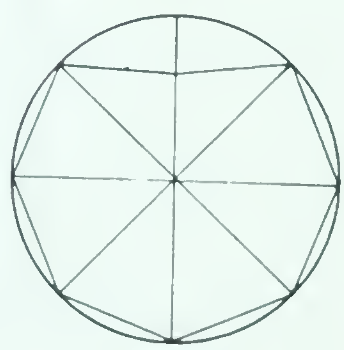

2090

TABLE a15

Hybrid index values of _Betula papyrifera_, _B. pumila_ var. _glandulifera_ and hybrids.

Character	Range	Index number
Leaf length (cm)	Less than 2.5	0
	2.5 - 3.5	1
	3.6 - 4.5	2
	4.6 - 5.5	3
	More than 5.5	4
Widest point of leaf	Above the mid-point	0
	At the mid-point	1
Number of teeth on one side of one leaf	Less than 15	0
	15 - 20	1
	21 - 30	2
	More than 30	3
Impression	_B. pumila_ var. _glandulifera_	0
	Hybrid	1
	B. papyrifera	2
Pairs of lateral leaf veins	Less than 5	0
	5 - 6	1
	6.1 - 7	2
	7.1 - 8	3
	More than 8	4
Leaf epidermis	Glabrous below	0
	Pubescent in axils of veins below	1
Branchlet glands	Present	0
	Absent	1
Margin of leaf	Crenate	0
	Crenate-serrate	1
	Serrate	2
	Partly doubly-serrate	3
	Doubly-serrate	4
Leaf tip	Round	0
	Round-acute	1
	Acute	2
	Acuminate	3

TABLE a16

Frequency distribution of mean stomatal length (μ) in *Betula papyrifera*, *B. pumila* var. *glandulifera*, and hybrid populations.

Size class (μ)	Number of individuals		
	Betula pumila var. *glandulifera*	*B.* x *sandbergii*	*B. papyrifera*
21.1-23.0	1	-	1
23.1-25.0	4	3	2
25.1-27.0	2	1	3
27.1-29.0	1	2	4
29.1-31.0	1	-	1
31.1-33.0	-	-	3
33.1-35.0	-	1	2
35.1-37.0	-	-	1
Total	9	7	17

TABLE a17

Names, synonyms, and reported chromosome numbers of some species of *Betula*.

Name	Synonyms	Chromosome number	Authors
B. fontinalis	*B. occidentalis* *B. rhombifolia* *B. microphylla* var. *fontinalis* *B. microphylla*	28	Packer, 1964 unpublished; (Dugle)
B. fontinalis var. *piperi*	*B. piperi*	28	Woodworth, 1931
B. glandulosa	*B. nana* var. *intermedia* *B. glandulosa* var. *glandulosa* *B. glandulifera*	28	de Pouques, 1949; Packer, 1964; (Dugle)
B. pumila		56	Woodworth, 1931
B. pumila var. *glandulifera*	*B. glandulifera* *B. glandulosa* var. *glandulifera* *B. hallii* *B. obovata*	56	Woodworth, 1931 Löve and Löve, 1964 (Dugle)
B. resinifera	*B. papyrifera* var. *neoalaskana* *B. neoalaskana* *B. alaskana* *B. papyrifera* var. *humilis* *B. alba* subsp. *papyrifera* var. *humilis*	28	

Table a17, continued.

Name	Synonyms	Chromosome number	Authors
B. papyrifera	B. papyracea	70	Woodworth, 1931
	B. alba var. papyrifera	70-84	Johnsson, 1949 (Dugle)
	B. alba subsp. papyrifera var. communis	70,84	Brittain, 1964 unpublished
		56-84	(Dugle)
	B. papyrifera var. occidentalis	84	Woodworth, 1931
	B. papyrifera var. commutata		
B. papyrifera var. cordifolia	B. cordifolia	56	Woodworth, 1931
B. x uliginosa	B. pumila var. glandulifera x B. resinifera	28-56	
B. x sargentii	B. glandulosa x B. pumila var. glandulifera	28-56	
B. x eastwoodae	B. glandulosa x B. fontinalis	28	
B. x utahensis	B. fontinalis x B. papyrifera	28-84	
	B. andrewsii		
	B. subcordata		
	B. montanensis		
	B. papyrifera var. subcordata	56	Woodworth, 1931
	B. x conmixta		
	B. papyrifera var. montanensis		

Table a17, continued

Name	Synonyms	Chromosome number	Authors
_B_. x _arbuscula_	_B_. x _sargentii_ x _B_. _papyrifera_	28-84	
_B_. x _winteri_	_B_. _resinifera_ x _B_. _papyrifera_	28-84	
_B_. _kenaica_	_B_. _papyrifera_ var. _kenaica_	70 c 65	Woodworth, 1931
_B_. _ermanii_		56	Johnsson, 1945; Grant, 1964
_B_. _utilis_		28	Flovik, 1940
_B_. _utilis_ var. _prattii_		28	Woodworth, 1931
_B_. _albo-sinensis_		56	Johnsson, 1945
_B_. _costata_			
_B_. _nigra_		28	Woodworth, 1931 Flovik, 1940
_B_. _lenta_		28	Woodworth, 1929, 1931
_B_. _lutea_		84	Woodworth, 1931
_B_. _verrucosa_	_B_. _alba_ subsp. _verrucosa_	28	Helms and Jorgensen, 1927; Woodworth, 1929, 1931; Johnsson, 1945, 1949; Löve, 1944, 1954; Natho, 1959
		42	Johnsson, 1944
	_B_. _pendula_	28	Woodworth, 1931; Natho, 1959
	_B_. _alba_		
	_B_. _pendula_ f. _atrata_	c 42	Natho, 1959

Table a17, continued

Name	Synonyms	Chromosome number	Authors
B. pubescens		56	Helms and Jorgensen, 1927; Woodworth, 1931, dePouques, 1949; Natho, 1959
B. callosa	*B. pubescens* subsp. *callosa*	56	Löve and Löve, 1948, 1956
B. carpatica	*B. pubescens* subsp. *carpatica*	56	Natho, 1959
B. populifolia		28	Woodworth, 1931 Flovik, 1940
B. nana		28	Wetzel, 1928, 1929; Jaretzky, 1930; Flovik, 1940
B. excelsa		56	Grant, 1964
B. fruticosa		56	dePouques, 1948
B. alleghanensis		84	Woodworth, 1929, 1930, 1931
B. humilis		28	Jaretzky, 1930; Natho, 1959
B. davurica	*B. dahurica*	c 90	Woodworth, 1931
		56	dePouques, 1949
B. coerulea-grandis		28	Woodworth, 1931
B. japonica	*B. platyphylla*	28	Woodworth, 1931; Johnsson, 1949; dePouques, 1949
B. maximowicziana		28	Woodworth, 1931
B. x *jackii*	*B. pumila* x *B. lenta*	42	Woodworth, 1931

Table a17, continued

Name	Synonyms	Chromosome number	Authors
_B_. x _purpusii_	_B_. _lutea_ x _B_. _pumila_ var. _glandulifera_	70	Woodworth, 1931
_B_. x _intermedia_	_B_. _pubescens_ x _B_. _nana_		
_B_. x _aurata_	_B_. _pubescens_ x _B_. _verrucosa_	42	Johnsson, 1945
		56	Johnsson, 1945
	_B_. _pubescens_ x _B_. _pendula_	42	Natho, 1959
_B_. x _fennica_	_B_. _nana_ x _B_. _verrucosa_		
_B_. x _koehnei_	_B_. _verrucosa_ x _B_. _papyrifera_	56	Johnsson, 1945, 1949
_B_. x _coerulea_	_B_. _coerulea-grandis_ x _B_. _populifolia_	28	Woodworth, 1931
_B_. x _borggreveana_	_B_. _papyrifera_ x _B_. _pumila_		
_B_. x _hornei_	_B_. _nana_ x _B_. _papyrifera_		